

Bothalia

A JOURNAL OF BOTANICAL RESEARCH

Vol. 39,1

May 2009

TECHNICAL PUBLICATIONS OF THE SOUTH AFRICAN NATIONAL BIODIVERSITY INSTITUTE PRETORIA

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Volume 39,1

Scientific Editor: G. Germishuizen
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2 Cussonia Avenue, Brummeria, Pretoria
Private Bag X101, Pretoria 0001

ISSN 0006 8241

May 2009

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Date of publication of *Bothalia* 38,2: 14 October 2008.

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New species of *Moraea* (Iridaceae: Iridoideae), with range extensions and miscellaneous notes for southern African species

P. GOLDBLATT* and J.C. MANNING**

Keywords: Iridaceae, Iridoideae, *Moraea* Mill., new species, southern Africa, taxonomy

ABSTRACT

Three new species are described in the largely sub-Saharan genus *Moraea* Mill. (± 200 spp.), all from its centre of diversity in the winter rainfall region of southern Africa. *Moraea pearsonii*, from Hottentotskloof near Ceres in Western Cape, flowers in late November and December when its leaves are $\pm$ dry, and has small, pale lilac, stellate flowers with the style branches each divided to the base into filiform arms. *Moraea tanquana*, from the Tankwa River Basin in Northern Cape, resembles the southern Namaqualand *M. deserticola* but has broad, plane leaves, short anthers exerted from a shallower floral cup and a short style. In section *Acaules*, *M. longipes* from Namaqualand stands out in its early flowering habit, a stem consisting of a single long internode reaching well above the ground, short style and unusually long anthers. *Moraea jarmilae* described from Ox Bow, Lesotho in 2002, is conspecific with *M. albicuspa* and is reduced to synonymy. Significant range extensions are reported for *M. elsiae*, *M. falcifolia*, *M. pseudospicata*, *M. spathulata*, *M. tricolor*, *M. vegeta*, *M. verecunda*, *M. vespertina* and *M. vlokii*. A yellow-flowered morph, local in the Perdebont Valley of the Little Karoo, is reported for the first time in typically blue- to violet-flowered *M. bipartita*, as well as the occurrence of a hybrid swarm, rare in *Moraea*, between *M. bipartita* and *M. polyanthos*.

INTRODUCTION

The old world and largely sub-Saharan genus *Moraea* Mill. (Iridaceae: Iridoideae) comprises some 200 species of cormous geophytes. Although florally diverse, *Moraea* is recognized in Iridoideae by a bifacial, channelled (rarely terete) leaf blade and corms of a single internode derived from a lateral bud. Most species have iris-like flowers with flattened, petaloid style branches, with filaments at least partially united. Other floral types make exact definition of the genus difficult. *Moraea* is most diverse in southern Africa and has a marked concentration of species in the winter rainfall region of western South Africa and adjacent southwestern Namibia, the likely area of origin of the genus (Goldblatt *et al.* 2002). Here we describe three new species. *Moraea pearsonii* from Hottentotskloof, near Karooport in the Ceres District, was re-collected in 2007 for the first time since its discovery 99 years ago, when H.H.W. Pearson gathered fragmentary material in November 1908. A late flowering species, it blooms in November and late December, and the small, stellate flowers have unusual, filiform style branches each divided to the base. This style conformation appears to have evolved independently four times in the genus. *Moraea tanquana* from the Tankwa National Park, is allied to *M. deserticola* Goldblatt from southern Namaqualand and *M. speciosa* (L.Bolus) Goldblatt from the Western Karoo, and shares with these species, cup-like, blue to mauve flowers with subequal tepals. Although superficially resembling *M. deserticola*, it differs from that species in the short anthers exerted from the floral cup and short style dividing opposite the anther bases so that the style branches emerge between the anthers. In section *Acaules*, *M. longipes* from Namaqualand stands out in its early flowering, aerial stem

consisting of a single long internode reaching well above the ground, short style and unusually long anthers. Of these new species all but *M. longipes* are currently known from a single locality but we suspect that collecting nearby at the appropriate times of the year, will show them all to have wider ranges.

We take this opportunity to reduce *Moraea jarmilae* J.J.Halda, described in 2002 from Ox Bow in Lesotho, to synonymy in *M. albicuspa* Goldblatt, and to report significant range extensions for several southern African species. Populations of the southwestern Cape species *M. elsiae* Goldblatt and *M. tricolor* Andrews have been discovered in the vicinity of Stilbaai in the southern Cape, range extensions of 100 km or more from their next nearest stations. The Stilbaai populations of *M. tricolor* also exhibit a shift in flowering time and habitat, unprecedented in *Moraea*. The widespread eastern southern African *M. spathulata* (L.f.) Klatt is now known from the higher mountains of the Great Karoo, a surprising record for a plant of otherwise mesic coastal and montane grassland habitats. A population that we refer to *M. vespertina* Goldblatt & J.C.Manning, a species until now known from two localities on the Bokkeveld Plateau west of Calvinia, has been discovered in the Tankwa National Park, some 200 km to the south. Although differing in some respects from the Bokkeveld populations, notably their slightly larger flowers and drier habitat, the Tankwa plants seem best included here for the moment.

We also report range extensions for *Moraea falcifolia* Klatt, *M. pseudospicata* Goldblatt, *M. spathulata*, *M. vegeta* L., *M. verecunda* Goldblatt and *M. vlokii* Goldblatt, the last-named species known until now from a small portion of the Swartberg. For *M. tricolor*, we report for the first time, capsule and seed shape, and compare these characters with closely related *M. ciliata* (L.f.) Ker Gawl. in which seeds and capsules are unusually variable but appear to be correlated with flower colour. For *M. bipartita* L.Bolus we document the existence of yellow-flowered populations in an otherwise blue- to

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MS. received: 2008-05-27.

violet-flowered species, and discuss the presence of a hybrid swarm between *M. bipartita* and closely allied *M. polyanthos* L.f. Lastly, we discuss a likely new species from Namibia, too inadequately known to formally describe and name.

NEW SPECIES AND TAXONOMIC ADJUSTMENTS

1. *Moraea pearsonii* Goldblatt & J.C.Manning, sp. nov.

Plantae 200–450 mm altae ex corno globoso 20–30 mm diam. profunde sub terram infosso, tunicis ex fibris nigris constantibus, folio producto solitario linearicaniculato marginibus involutis 2–3(–4) mm lato ad 1 m longo, caule erecto ramoso ramis ultimis rhipidia sessilia ferentibus, spathis siccis, floribus pallide lilacinis externe pallidis bubalinis inodoris, tepalis $\pm$ 14 mm longis, externis 4.5–5.0 mm latis internis $\pm$ 4 mm latis unguibus 1.0–1.5 mm longis, filamentis liberis ad basem contiguus 3.5–4.0 mm longis suberectis malvinis, antheris 4.5–5.0 mm longis flavis, stylo filiformi malvino $\pm$ 2.5 mm longo, ramis styli ad basem furcatis in brachia filiformia duo 3.5–4.0 mm longa productis, capsula doliformi 4–5 $\times$ 3–4 mm.

TYPE.—Western Cape, 3319 (Worcester): Farm Vrede, dry wash west of junction between Touwsrivier and Ceres–Sutherland roads, (–BA), 15 December 2007, Manning 3128 (NBG, holo.; K, MO, iso.).

Plants 200–450 mm high. *Corm* globose, 20–30 mm diam., deeply buried; tunics of coarse black fibres, drawn into finely fibrous neck up to 150 mm long. *Stem* erect, usually with 1–4 suberect branches at upper nodes, dull purplish where exposed; branches with (1–)4–6 sessile lateral flower clusters. *Foliage leaf* solitary, basal, much longer than stem, trailing, linear and channelled but margins inrolled when dry and thus appearing terete, 2–3(–4) mm wide and up to 1 m long, partially or entirely dry at flowering, leathery; cauline leaves bract-like and entirely sheathing, dry and papery, attenuate margins united in lower half. *Spathes* dry and papery at flowering, pale buff or lightly flushed with purple, attenuate, inner 20–33 mm long, outer $\pm$ as long as inner. *Flowers* pale lilac flushed buff on reverse; tepals with small, transversely oblong, yellow nectar guides at limb bases, unscented, shortly clawed, nectar erect, 1.0–1.5 mm long, apressed to base of filaments, limbs spreading or slightly reflexed, oblong-elliptical, outer broader, 13 $\times$ 4.5–5.0 mm, inner 13 $\times$ 4 mm. *Stamens* free; filaments contiguous at base, 3.5–4.0 mm long, suberect, mauve; anthers erect, 4.5–5.0 mm long, yellow, curving inwards distally at anthesis. *Ovary* ovoid, 2.5–3.0 mm long; style erect, filiform, $\pm$ 2.5 mm long, mauve, branches spreading to ascending between anthers, divided to base into two filiform arms 3.5–4.0 mm long. *Capsules* barrel-shaped, 4–5 $\times$ 3–4 mm. *Seeds* angled by pressure, $\pm$ 1.5 mm diam., reddish brown, testa surface rugulose. *Flowering time*: late November to late December; flowers opening at $\pm$ 17:30 and wilting at $\pm$ 20:30. Figure 1.

Distribution and ecology: *Moraea pearsonii* is currently known only from the roadside between Hottentotskloof Farm and Karoopoort (Figure 2), almost midway

between the towns of Ceres and Touws River. Plants grow in sandy alluvium over shale in washes at the foot of the Baviaansberg, the southernmost extremity of the Swartruggens, in open shrubland transitional between renosterveld and arid fynbos.

Flowering in *Moraea* is typically in the wet season, which is summer in eastern, southern and tropical Africa, and late winter and spring in western southern Africa and southwestern Namibia. A significant number of species, however, exhibit a shift in their flowering to the dry season, although they tend to produce their leaves in the wet season when conditions are optimal for vegetative growth. Examples of such species include the eastern African *M. stricta* Baker, which blooms in August to October but produces its leaf in November, and *M. pseudospicata* from southwestern South Africa, which flowers from December to February when the leaves are dry and brown, only producing new foliage leaves in May. *M. pearsonii* has a similar ecology, and the rather leathery leaves are mostly dry by early summer when flowering takes place. The pale lilac flowers open in the late afternoon between 17:30–18:00, and last for just three hours before withering at sunset. The lack of floral scent, absence of evident nectar, and the prominently positioned anthers, suggest that *M. pearsonii* is adapted for pollination by pollen-collecting bees.

Diagnosis and relationships: *Moraea pearsonii* has a single, long, trailing leaf up to 1 m long, linear and channelled when fresh but with the margins involute on drying so that the leaf then appears to be terete. The corm, deeply buried among the rocky alluvium up to 20 cm below the surface and thus difficult to extract, has a tunic of coarse, black fibres. The branched inflorescences bear numerous sessile lateral flower clusters of pale lilac, stellate flowers, 20–25 mm in diameter. These open exceptionally late in the day, and until the tepals unfold at $\pm$ 17:30 the plant is virtually invisible in the dry, light brown vegetation. Structurally the flowers resemble those of the *Hexaglottis* group of *Moraea* (Goldblatt & Manning 2000), with the style branches each divided to the base into thread-like arms extending between the stamens. In addition, the tepals are subequal, with short claws and spreading limbs, and free filaments. The *Hexaglottis*-type flower is typical of several species of *Moraea*, notably among the six, pale yellow-flowered species of section *Hexaglottis* (Vent.) Goldblatt, previously recognized as the genus *Hexaglottis* Vent. until merged in *Moraea* (Goldblatt 1987, 1998). It is also known in the yellow-flowered *M. nana* (L.Bolus) Goldblatt & J.C.Manning of section *Tubiflora* Goldblatt; and in the taxonomically isolated, blue-flowered Namibian *M. hexaglottis* Goldblatt of section *Moraea* (Goldblatt 1986a). Based on vegetative morphology, we conclude that *M. pearsonii* is not allied to any of these species but belongs in section *Polyanthes* Goldblatt, and more precisely with the blue- to lilac- or mauve-flowered *M. crispa* alliance of western South Africa. Within this group, it is perhaps most closely allied to *M. pseudospicata*, which has a similar branching pattern with sessile rhipidia, similar corm tunics of coarse black fibres, and it also flowers late in the season when the leaves are $\pm$ dry (Goldblatt 1986a). The style branches of this species are more typical of *Moraea*, being flattened and forked only at the tips and the filaments are united basally.



FIGURE 1.—*Moraea pearsonii*, Manning 3128 (NBG): A, corm and flowering stem; B, flower with two tepals removed; C, inner (left) and outer (right) tepals; D, style branches; E, capsules; F, seed. Scale bar: A, E, F, 10 mm; B, C, 5 mm; D, 2.5 mm. Artist: John Manning.

History: the species was first collected by H.H.W. Pearson, Professor of Botany at the South African College (later the University of Cape Town) in late November 1908 during an expedition from Cape Town to Namibia. Pearson collected just the inflorescence branches of a sin-

gle plant, in bloom close to the hottest time of the year. Although the floral spathes were dry at the time of collection, the rhipidia (flower clusters) bore flowers that had wilted that day or the previous one. His notes on the sheet (Pearson 4810) indicate that the flowers were

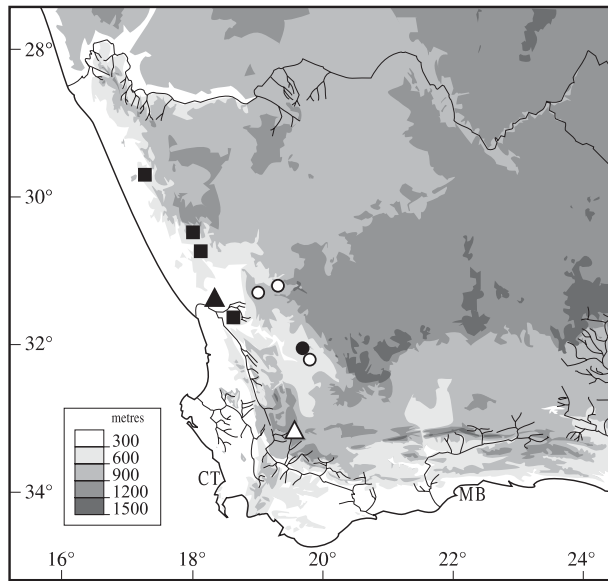


FIGURE 2.—Known distribution of *Moraea deserticola*, ▲; *M. pearsonii*, △; *M. tanquana*, ■; *M. vespertina*, ●; and *M. longipes*, ■.

blue, and examination of the withered flowers revealed that they had free filaments and slender style arms, thus unlike most *Moraea* species, which have the filaments united below and flattened style arms. More than that could not be determined from the available material and it remained impossible to identify the plant or even to draw up a satisfactory description. In December 2007, we mounted an expedition to try and locate the species, collected northeast of Ceres, between Hottentotskloof and Karooport. A small population of plants matching Pearson's original collection were located in just this area and confirmed that they represented an undescribed species.

Additional specimen examined

WESTERN CAPE.—3319 (Worcester): roadside between Hottentots Kloof and Karoo Poort, (–BA), 29 November 1908, Pearson 4810 (K).

2. *Moraea tanquana* Goldblatt & J.C.Manning, sp. nov.

Plantae ad 0.5 m altae ex cormo subgloboso, tunicis ex fibris crassis atrobrunneis usque nigris constantibus, foliis 3 infimo basali lineari canaliculato 2–5 mm lato superioribus caulibus, caule usque 3-ramoso, spathis herbaceis ad apicem siccis attenuatis interiore $\pm$ 30 mm longa, floribus pallide caeruleis vel malvinis cum cupula flava, tepalis exterioribus obovatis $\pm$ 25 mm longis limbis 15–16 $\times$ 12 mm, interioribus $\pm$ 22 mm longis, filamentis $\pm$ 10 mm longis in columnam connatis, antheris contiguis ad anthesin 5 mm longis postea $\pm$ 3 mm longis luteis, ramis styli $\pm$ 1 mm longis antheris obtectis, lobis stigmatibus bifidis sine cristis.

TYPE.—Northern Cape, 3219 (Wuppertal): Tankwa National Park, small koppie east of Leeuberg, 404 m, (–BB), 4 August 2006, Steyn 872 (NBG, holo.; PRE, iso.).

Plants up to 0.5 m. *Corm* subglobose, $\pm$ 20 mm diam.; tunics of coarse, dark brown to blackish fibres. *Stem* up

to 3-branched from upper nodes; branches subtended by sheathing, attenuate, bract-like cauline leaves. *Cataphylls* pale and membranous. *Leaves* 3, lowermost basal, linear and channelled, 2–5 mm wide, $\pm$ three quarters as long as stem, upper 2 leaves cauline, $\pm$ as long as the basal. *Spathes* green but dry and membranous apically with brownish cusps; inner $\pm$ 30 mm long, outer $\pm$ half as long as inner. *Flowers* pale blue or mauve with a yellow cup, and small, rounded, yellow nectar guides on all tepals at mouth of cup, tepal claws minutely puberulous at base, 8–9 mm long, ascending and forming wide cup, limbs spreading horizontally; outer tepals obovate, $\pm$ 25 mm long, limb 15–16 $\times$ 12 mm, inner tepals slightly shorter, $\pm$ 22 mm long. *Stamens* with filaments $\pm$ 10 mm long, reaching to mouth of floral cup or exserted $\pm$ 1 mm, united, column cylindrical, minutely puberulous at base; anthers erect, contiguous, 4–5 mm long at anthesis but shrinking to 3 mm after dehiscence, yellow, appressed to and concealing style. *Ovary* ovoid, 4–5 mm long, exserted from spathes, uniformly pale green; style branching at top of filament column, branches $\pm$ 1 mm long, concealed by anthers; stigma lobes bifid, crests lacking. *Capsules* and *seeds* unknown. *Flowering time*: August, probably also in late July. Figure 3.

Distribution and ecology: *Moraea tanquana* is known from a single hill in the Tankwa Karoo National Park east of Leeuberg (Figure 2). The colony was found on a dolerite outcrop and comprises numerous plants.

Diagnosis and relationships: *Moraea tanquana* is most likely allied to *M. deserticola* from the Knersvlakte and the more widespread *M. speciosa* of the Western Karoo (Goldblatt 1986b). All three have upright stems bearing multiple leaves, branched stems, cup-shaped, pale blue to mauve flowers with nearly equal tepals, contiguous anthers carried on a slender, cylindrical filament column and style branches lacking crests. They differ in several vegetative and floral characteristics (Table 1). *M. speciosa*, most robust of the three, has several, broad foliage leaves up to 40 mm wide, tepals 35–45 mm long, anthers (8–)12–17 mm long, and the style divides between the middle and apex of the anthers; when fully extended the style branch tips typically exceed the anthers. Smaller *M. deserticola* has narrow foliage leaves 2–3 mm wide, tepals 30–36 mm long, anthers 6.0–6.5 mm long (shrinking after anthesis to 5 mm) that remain contiguous around the style. The style itself divides at or just beyond the anther tips into short branches $\pm$ 1 mm long that are carried above the anthers. In contrast, *M. tanquana* has foliage leaves up to 5 mm wide, tepals $\pm$ 22 mm long, short anthers, 4–5 mm long, that exceed the style? and enclose them. The style divides opposite the lower third of the anthers so that the stigmatic tips of the short style branches, $\pm$ 1 mm long, emerge from between the middle of the $\pm$ contiguous anthers. The flower of *M. tanquana* most closely resembles that of *M. deserticola* in general aspect, but its shorter anthers are held beyond the floral cup, whereas the anthers are longer in *M. deserticola* and their bases are retained within the floral cup.

Vegetatively *Moraea deserticola* also differs from *M. tanquana* in its $\pm$ membranous spathes, the longer inner spathe 30–40 mm long, whereas in *M. tanquana* the spathes are green with dry attenuate tips and the



FIGURE 3.—*Moraea tanquana*, Steyn 872 (NBG): A, corm and flowering stem; B, stamens and style; C, style branches. Scale bar: A, 10 mm; B, 4 mm; C, 2.5 mm. Artist: John Manning.

inner spathe is ± 30 mm long. The ovary is conspicuously veined with dark red in *M. deserticola* thus unlike the uniformly green ovary of *M. tanquana*. Edaphically the two also differ: *M. deserticola* occurs in the Knersvlakte to the northwest and favours light, loamy clay surrounding limestone outcrops, quite dif-

ferent from the dolerite outcrops and heavy clay soils in which *M. tanquana* grows.

3. *Moraea longipes* Goldblatt & J.C.Manning, sp. nov.

Plantae 100–180 mm altae, caule eramoso supra terram bene extenso, cormo globoso 15–20 mm diam., tunicis ex fibris crassis pallidis constantibus oblecto, foliis 2 (spathis externis exclusis) suboppositis rectis 45–85 mm longis canaliculatis marginibus laevigatis vel parce ciliatis, rhipidium floribus nonnullis; spathis 50–70 mm longis, subaequalibus vel spatha externa paulo maiore, floribus pallide flavis vel $\pm$ albis tepalis internis cupreis, tepalis externis ± 30 mm longis unguibus ± 10 mm longis munitis, limbis $\pm$ patentibus, tepalis internis ± 28 mm longis, filamentis 7–9 mm longis basin versus per ± 1.5 mm connatis, antheris 7.7–9.0 mm longis, stylo ± 1 mm longo, ramis styli 13–16 mm longis, cristis 8–10 longis, anguste triangularibus.

TYPE.—Western Cape, 3118 (Vanhynsdorp): Namaqualand, 6 km NW of Bitterfontein on Kotzesrus road, in stony granitic ground, (–AA), 1 June 2008, Manning 3172 (NBG, holo.; MO, iso.).

Plants 100–180 mm high, base surrounded by a well-developed fibrous collar. *Corm* globose, 15–20 mm diam., tunics of $\pm$ straw-coloured, coarse fibres often with thickened vertical ridges. *Stem* unbranched, consisting of single internode extending from corm to well above ground level. *Leaves* 2 (excluding opposed leaf-like spathes enclosing flowers), subopposite, inserted at base of spathes, suberect, straight, 45–85 mm long, channelled, paler green adaxially; margins smooth or sparsely ciliate. *Rhipidium* several-flowered; spathes subequal, or outer slightly larger, clasping inner for $\pm$ half its length, 50–70 mm long, inner with broad, transparent membranous margins. *Flowers* pale yellow or translucent white with pale copper inner tepals, margins of outer tepals and on reverse of tepals; nectar guide yellow speckled with black dots; tepals unequal, outer ± 30 mm long, claw suberect, ± 10 mm long, hairy in midline, limb $\pm 20 \times 19$ mm, laxly spreading, hairy toward base, inner tepals $\pm 28 \times 2$ –4 mm, claws suberect, ± 9 mm long, limbs spreading. *Stamens* with filaments suberect, 7–9 mm long, united basally for ± 1.5 mm; anthers appressed to style branches, 7.5–9 mm long, reaching base of stigma lobes. *Ovary* elongate, fertile part ovoid, 5–9 mm long, usually at least partly included; style dividing ± 1 mm above base, branches ascending, 13–16 mm long; stigma lobe rounded; crests erect, narrowly triangular, outer margins slightly and unevenly serrated, 8–10 mm long, 2.5–3 mm wide at base. *Capsules* and *seeds* unknown. *Flowering time*: late May to early July. Figure 4.

Distribution and habitat: Namaqualand, from Springbok in the north to the Gifberg Flats in the south; on granitic or sandy gravel flats (Figure 2).

Diagnosis and relationships: a member of section *Acaules*, *Moraea longipes* has the general aspect of *M. ciliata* and *M. tricolor* except that the stem is not subterranean at flowering but extends up to 180 mm above the ground. Like most species of the section, the ovary is retracted to the base of the inflorescence spathes after

TABLE 1.—Comparison of flowers of *Moraea tanquana*, *M. deserticola* and *M. speciosa*. All measurements were taken from fresh material. Anthers measured before anthesis

Character	<i>M. tanquana</i>	<i>M. deserticola</i>	<i>M. speciosa</i>
Spathe length (mm)	± 30	33–40	50–70
Outer tepals length (mm)	± 25	30–36	35–45
Tepal claws length (mm)	8–9	12	12–15
Perianth colour	blue with yellow cup	pale slate-blue with white cup	blue to grey-blue with white to yellow cup
Floral cup depth (mm)	± 9	± 12	10–12
Filament length (mm)	± 10	8–10	10–13
Anther length (mm)	4–5	6.0–6.5	12–17
Style branches (mm)	± 1	± 1	2–6
Point of division of style branches	opposite lower third of anthers	opposite anther tips or beyond them	opposite middle to upper third of anthers

flowering. The flowers are most like those of *M. ciliata* but have slightly broader style crests, triangular with the base 2.5–3.0 mm wide ($\pm$ linear in *M. ciliata*) and the filaments are united basally for $\pm$ 1.5 mm, about one fifth of their length. In other species of the section, the filaments are united for one third to half their length. The anthers of *M. longipes* are also the longest in the section, measuring 7.5–9.0 mm. A unique feature in the section is the collar of fibres around the underground part of the stem, this alone making *M. longipes* easily recognized even without flowers. The species flowers early in the season, May to early July, and grows in places where *M. ciliata* has been found in bloom six to eight weeks later. Flower colour in *M. longipes* is either pale, watery yellow or translucent white, then with the edges of the outer tepal limbs and the inner tepal limbs a bright copper colour and with the tepals flushed deep copper on the reverse. Like other members of section *Acaules*, the flowers are fugaceous and last just one day.

Examining the ovary of *Moraea longipes* closely, we noted that there is no line of abscission at its base as in most other species of *Moraea*. After examining other members of the section, we found they too lack this abscission line, which elsewhere in the genus is the point at which unfertilized ovaries are abscised. We tentatively suggest that the so-called pedicel of the flower in section *Acaules* may actually be part of the ovary and that the flowers then lack a true pedicel. In freshly open flowers of *M. ciliata* and *M. tricolor*, the ovary stalk is hollow and contracts in faded flowers, then becomes closely wrinkled as the tissue collapses on itself, then draws the ovule-containing part of the ovary into the lower part of the spathes. Anatomical comparison of true pedicels of *Moraea* species with those of the ovary stalk of section *Acaules* may solve this question.

Additional specimens examined

NORTHERN CAPE.—2917 (Springbok): Sanagas, near Springbok, (–DC), 4 June 1980, *Dryfhout* 2788 (NBG). 3117 (Lepelfontein): Namaqualand, 15 km SE of Kotzesrus, Farm Biesiesfontein, in stony granitic gravel, (–BB), 1 June 2008, *Manning* 3173 (NBG).

WESTERN CAPE.—3018 (Vanrhynsdorp): Matsikamma, (–DB), 16 June 1983, *Snijman* 714 (NBG).

4. *Moraea albicuspa* Goldblatt in *Annals of the Missouri Botanical Garden* 64: 230 (1973). Type: South Africa, [KwaZulu-Natal], Drakensberg, source of the Tina River, March 1904, *Galpin* 6846 (BOL, holo.!; PRE!, SAM!, iso.).

M. jarmilae J.J.Halda: 69, fig. 79 (2002). Type: Lesotho, Drakensberg in the vicinity of Ox Bow, $\pm$ 3 100 m, 10 March 1989, J.J. & J. Haldovi s.n. PR4710 (PR, holo.!), syn. nov.

Moraea jarmilae was described for plants from Ox Bow in Lesotho that had unusual fringed edges to the outer tepals, which were otherwise $\pm$ lanceolate in shape. The inner tepals were described as tricuspidate and greenish (Halda 2002) and the species was likened to the Mpumalanga and northern KwaZulu-Natal species, *M. pubiflora*, with the notable exception of the fringed tepal limbs, but *M. pubiflora* has the outer tepals velvety on the reverse, a feature not noted for *M. jarmilae*. The type specimen, however, clearly shows the inner tepals to be linear and apically undivided. Tepals of this shape are known among Drakensberg *Moraea* species only in *M. albicuspa*, which has white flowers, the outer tepal claws with a linear, yellow nectar guide. We are confident that *M. jarmilae* represents plants with abnormally formed outer tepal limbs, possibly due to foraging by an insect while in bud. We accordingly reduce the species to synonymy in *M. albicuspa*, which has previously been collected in Lesotho from Sehlabathebe, southeast of Ox Bow, and is known from Giant's Castle in the central high Drakensberg of KwaZulu-Natal southwards along the escarpment to Engcobo in Eastern Cape.

RANGE EXTENSIONS AND MISCELLANEOUS NOTES

Moraea bipartita L.Bolus

This widespread species extends from the Swellendam District in the west through the Little Karoo and part of the southern Cape to Uitenhage in the east (Goldblatt 1986a). Over much of its range, plants have blue to violet flowers of the standard *Moraea*-type, thus with larger outer tepals bearing nectar guides at the base of the limb, filaments united for half their length, and a style dividing at the apex of the filament column into three petaloid branches that terminate in prominent, paired, erect crests. The stigmatic lobe lies at the base of the crests on the abaxial surface of the style branch, and in *M. bipartita* is bilobed, as in many species of the genus. The species is distinguished among its allies in section *Polyanthes* by the presence of several (at least three) channelled foliage leaves, a branched stem, and relatively small flowers. Plants with yellow flowers discovered by ecologist J. Vlok in the Perdebont Valley of the Little Karoo near the northern end of Robinson Pass south of Oudtshoorn, seemed worth investigating in view of the other-

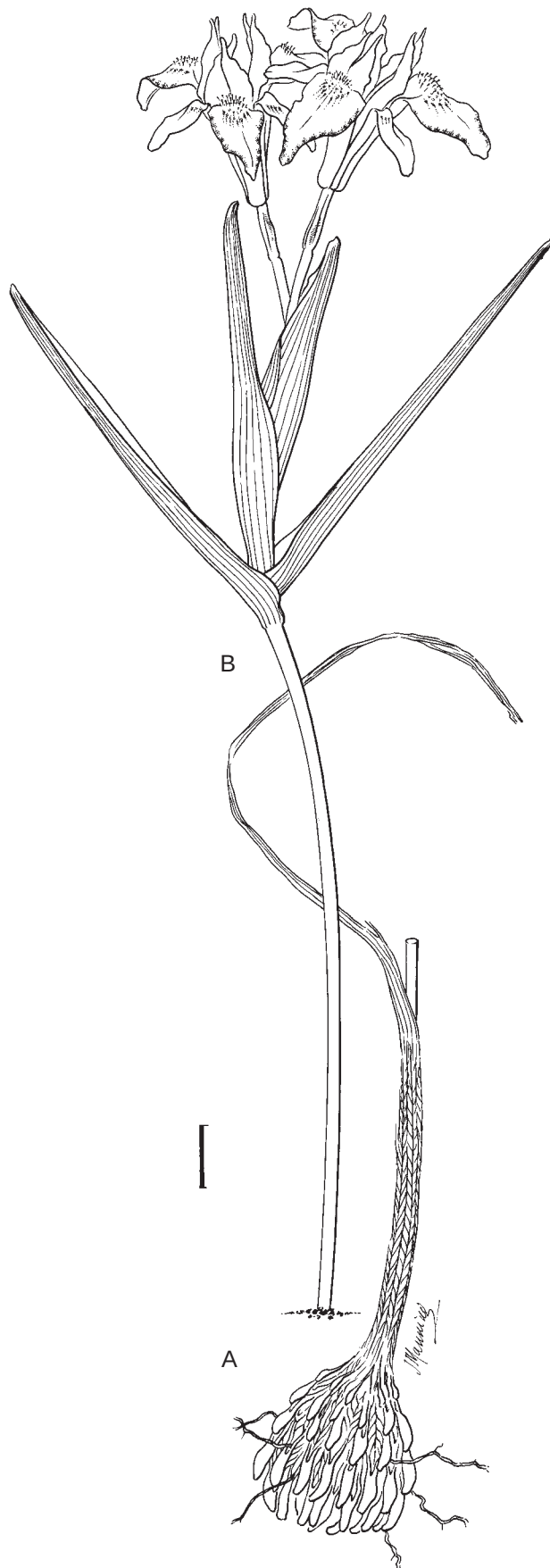


FIGURE 4.—*Moraea longipes*, Manning 3172 (NBG): A, corm. B, flowering stem and flowers. Scale bar: A, 10 mm; B, 4 mm. Artist: John Manning.

wise universal blue to violet flower colour not only in *M. bipartita* but in almost all members of section *Polyanthes* (*M. polyanthos* L.f. itself may have blue-mauve or white flowers). The yellow-flowered plants resembled typical *M. bipartita* so exactly when compared with typical blue-flowered plants found elsewhere the same day, that we were forced to conclude that colour was the only difference between these plants, growing on the Farm Safraanrivier (Goldblatt *et al.* 12955) and typical *M. bipartita*. *Moraea bipartita* then, may rarely have yellow flowers, a striking exception for section *Polyanthes*.

At the Safraanrivier site, yellow-flowered *Moraea bipartita* grew together with closely related *M. polyanthos*, a species distinguished from *M. bipartita* by flowers with subequal tepals, all with small nectar guides, and reduced style branches as wide as the anthers and without vestigial style crests. Hybrids between the two species were common and represent one of the few examples of a hybrid swarm in *Moraea*. A range of intermediate flower forms were represented among the hybrids, the most common of which had yellow or grey tepals with blue style branches, narrower than normal with smaller crests (Goldblatt *et al.* 12955A).

WESTERN CAPE.—3321 (Ladismith): northern foot of the Outeniqua Mountains in Perdebont Valley, Farm Safraanrivier, (–CC), 6 September 2007, Goldblatt, Vlok & Porter 12955 (NBG). Hybrids with *M. polyanthos*: loc. cit., Goldblatt, Vlok & Porter 12955A (NBG).

Moraea elsiae Goldblatt (1986a)

Moraea elsiae is one of several species of subgenus *Visciramosa*, an alliance distinguished by woody, rather than fibrous corm tunics, multiple foliage leaves, branched stems always viscid below the nodes, and flowers with filaments free but contiguous around the style (elsewhere in the genus the filaments are entirely connate or united in the lower half). Most species of the subgenus have typical *Moraea*-type flowers with outer tepals larger than the inner and with nectar guides at the base of the limbs, and flattened style branches bearing paired, petaloid crests. *M. elsiae* is an exception in having narrow style branches with vestigial crests and subequal tepals, all of which have nectar guides. The recorded range of *M. elsiae* is from the Cape Peninsula to the Potberg near Cape Infanta. The presence of the species has now been established in the Pauline Bohnen Reserve at Stilbaai, a range extension of some 100 km eastward.

WESTERN CAPE.—3421 (Riversdale): Stilbaai, Pauline Bohnen Reserve, (–AD), 20 October 2000, De V. Pienaar & Pienaar PB570 (NBG).

Moraea falcifolia Klatt

One of the most widespread of the winter rainfall *Moraea* species, *M. falcifolia* has been recorded from southern Namibia through Namaqualand south to the Breede River Valley and the western Little Karoo, as well as from Bushmanland and the Upper Karoo as far east as Kimberley. In Goldblatt's (1976, 1986a) revisions of the genus, no records were known from Eastern Cape or the central and eastern Little Karoo. Collections have now been made from the Little Karoo near Sebrasfontein in the northern foothills of the Outeniqua Mountains, in the Long Kloof, and from near Alexandria, thus

enlarging its already wide range significantly. Plants from these sites do not differ in any significant way from known collections.

WESTERN CAPE.—3322 (Oudtshoorn): low northern foothills of the Outeniqua Mountains near Sebrasfontein, (–CC), 13 July 1986, *Vlok 1518* (MO).

EASTERN CAPE.—3323 (Willowmore): Onder Kouga, off Long Kloof, (–DD), 28 September 1975, *Bayliss BS7098* (PRE). 3326 (Grahamstown): Salem–Alexandria road, Bushmans River Gorge, Longford Grange Farm, (–CB), 26 August 1995, *Dold & Cocks 1771* (GRA; MO, photo.).

Moraea pseudospicata Goldblatt (1986b)

When described, this late summer- and autumn-flowering species was known with certainty only from the Nieuwoudtville Wildflower Reserve and from Lokenburg, 30 km south of Nieuwoudtville. In March 1997, the species was found on the Nieuwoudtville Sports Ground and in March 2000 we found it to be common on Glenlyon Farm, now the Hantam National Botanic Garden, on soils derived from Dwyka tillite. Then in 2003 we discovered large numbers of what appeared to be *M. pseudospicata* in fruit on the Hantamsberg at Calvinia in areas that had been burned two years earlier. While flowers are not known for the Hantamsberg plants, they have the sessile lateral inflorescences, single linear leaf with tightly inrolled margins, and small, globose capsules that are diagnostic for *M. pseudospicata*. The species now seems to be common north and south of Nieuwoudtville in a belt along the western end of the Bokkeveld Plateau as well as inland on the Hantamsberg. The reasons for its apparent rarity are not only that it flowers in February, March and April when little collecting is done in this hot and summer-dry part of the Western Karoo, but also that the flowers only open late in the afternoon, after 16:00 and are until then virtually invisible except to the specialist collector. We suspect that *M. pseudospicata* has an even wider range than is currently documented.

NORTHERN CAPE.—3119 (Calvinia): Nieuwoudtville Sports Ground, (–AC), 31 March 1997, *Van Rooyen, Steyn & De Villiers 411* (NBG, PRU); Glenlyon Farm, renosterveld near reserve at entrance to farm property, (–AC), 13 March 2000, *Goldblatt 11305* (MO); Glenlyon Farm, renosterveld on road to Camel Kopie, (–AC), 13 March 2000, *Goldblatt 11305* (MO); Hantamsberg slopes, (–BD), 4 September 2002 (late fr.), *Goldblatt & Porter 12163* (MO, NBG, PRE).

Moraea spathulata (L.f.) Klatt

A widespread, eastern southern African species, *M. spathulata* extends from George in the southern Cape through eastern South Africa and Swaziland to eastern Zimbabwe, and is typically found in well-watered, montane habitats except at the extreme southern end of its range between George and Humansdorp where it occurs close to the coast. Exploration in the high mountains fringing the Great Karoo by E.G.H. Oliver in the 1970s and later by Ralph Clarke in 2005–2007, have resulted in the documenting of the species on the Koudeveldberge near Graaff-Reinet. Plants from the mountains of the Karoo differ in no way from those in the south at Knysna and Humansdorp, nor from those in the Drakensberg, despite the drier, and in winter, colder habitat. They constitute a remarkable range extension.

EASTERN CAPE.—3224 (Graaff-Reinet): Koudeveldberge SE of Doornbosch, (–AA), frequent scattered clumps on summit plateau and

north slopes with low tussock grass, 6 November 1974, *Oliver 5221* (NBG). 3225 (Somerset East): Sneeuberg above Suurkloof, Asante Sana Private Game Reserve, 1 800 m, (–AC), 6 December 2005, *Clarke & Coombs 155* (GRA).

Moraea tricolor Andrews

Until now, this southwestern Cape species has been recorded from Darling, the Malmesbury and Tulbagh Districts, historically from the Cape Peninsula (where it is now extinct), and locally in the Caledon District as far east as Napier (Goldblatt 1986a). A member of section *Acaules* Goldblatt (5 spp.), it has the acaulescent habit characteristic of the group, with flowers borne above the ground and then withdrawn by contractions of the stalk of the ovary to lie within the spathes and near ground level where the fruits mature. Within the section, *M. tricolor* is recognized by the broad, triangular style crests, 8–10 mm long and 4–5 mm wide at the base, usually with the filaments united for half their length, and often glabrescent foliage. Flower colour in *M. tricolor* ranges from pale yellow to pink, brick-red, violet or deep mauve-pink, always with prominent deep yellow nectar guides edged in darker pigment, often red or purple, at the base of the outer tepal limbs, hence the specific epithet *tricolor*. Collections from Stilbaai in the southern Cape (*Naudé s.n.*), where four separate populations are known (J. Naudé pers. comm. 2008), represents a range extension of some 150 km. These plants are also remarkable for flowering in May, whereas other populations of *M. tricolor* typically bloom in August and September, although plants have been collected in flower near Hopefield in June. The habitat of the Stilbaai populations, which grow in the well-drained sandy ground of coastal dunes, is unusual for the species, which typically favours seasonally moist to inundated, poorly drained sandy or clay flats. Despite the ecological shift and change in flowering time of the Stilbaai populations, we find no character of any taxonomic significance that permits their recognition. For the present we record the range extension and note the shift in ecology and flowering time.

Fruiting plants from Stilbaai (*Goldblatt, Manning & Naudé 11199*, MO, NBG) have capsules $9\text{--}12 \times \pm 6$ mm, and light brown, angular to subglobose seeds, $\pm 1.4 \times 2$ mm, with reticulate sculpturing. Capsules from one population of southwestern Cape *Moraea tricolor*, not recorded before, are 7–11 mm long and the seeds are also angular to subglobose with reticulate sculpturing and $1 \times \pm 1.3$ mm (*Goldblatt 11572*, MO). These seeds match those of most other species of the section except for small differences in size and are probably the plesiomorphic type for the section.

We also include a minor range extension for *Moraea tricolor* from Langebaan on Saldanha Bay, the northernmost record for the species (*Goldblatt & Porter 13066* (fl.), MO, NBG, 13210 (fr.), MO, NBG). Plants at this site have violet tepals with an orange rather than yellow nectar guide, colouring not before reported for the species. The capsules are ± 10 mm long, typical for the species.

Capsules and seeds of populations of *Moraea ciliata* (e.g., *Goldblatt & Porter 12710*, MO, 12691, MO) with yellow or white flowers, are similar in size and shape to those of *M. tricolor*, the seeds rather more angular and

often 5-sided, obscurely reticulate and $\pm 1 \times 1.5$ mm. Curiously, blue-flowered populations of the species that we have examined (e.g. *Snijman & Perry 2142*, NBG, in flower) have larger, globose seeds with less pronounced sculpturing and $2 \times 2-3$ mm, and are borne in elongate capsules 18–20 mm long (*Goldblatt et al. 12863*, MO). The variation in capsule and seed shape and size in colour morphs of *M. ciliata*, suggests differentiation among populations of the species associated not only with perianth colour but also capsules and seeds, and perhaps other features. Insufficient collections with capsules and fully developed seeds make more detailed exploration of this question impossible at this time.

WESTERN CAPE.—3318 (Cape Town): Langebaan, wet site in granite outcrop opposite post office, (–AA), 3 September 2008, *Goldblatt & Porter 13066* (MO, NBG), 28 September 2008, *Goldblatt & Porter 13201* (fr.) (MO, NBG). 3421 (Riversdale): Stilbaai, Geelkrans Nature Reserve, (–AD), May 2006, *Naudé s.n.* (NBG), 5 September 2007 (fr.), *Goldblatt, Manning & Naudé 12950* (MO, NBG); Stilbaai, Panorama Circle, 29 May 1980, *P. Bohnen 7542* (NBG); Stilbaai, grounds of The Gem Nursery, road from Stilbaai to Jongensfontein, 24 May 2003, *U. de V. Pienaar & A. Pienaar 378* (NBG).

Moraea vegeta L.

Locally common on the Cape Peninsula and recorded as far north as Darling and Hermon in the greater Malmesbury District, and as far east as Swellendam (*Goldblatt 1986a*), *Moraea vegeta* is a fairly inconspicuous species, with watery yellow or dull purple flowers. It is readily recognized by the several channelled, glaucous leaves and nodding, globose capsules with soft walls that show the outlines of the seeds. A new record from the Kobee Valley, some 250 km to the north is an unexpected and remarkable range extension. In the Kobee Valley, plants grow in sheltered kloofs and gullies in open bush dominated by wild olive (*Olea europaea* subsp. *africana*) on a west-facing slope above the valley floor. This is the only record of the species from the northwestern centre of the Cape flora region.

WESTERN CAPE.—3119 (Calvinia): Kobee Valley, gully on west-facing slopes above valley floor in light bush, (–CA), 1 September 2001, *Goldblatt & Porter 11801* (NBG).

Moraea verecunda Goldblatt

Although currently known from a few sites in the immediate vicinity of Nieuwoudtville (*Goldblatt 1986a*), specimens collected from south of the Bokkeveld Moun-

tains, on Uitkyk Pass descending into Biedouw Valley, appear to represent this species. The collection (*Stirton 11507*) has sessile lateral inflorescences, a solitary, narrow basal leaf, and small violet flowers with tepals 10–12 mm long, and partially fused filaments. No capsules are fully developed but the ovaries are fusiform and one immature capsule is beaked. These features accord exactly with *M. verecunda* and we tentatively treat this as a range extension for the species. A photograph (R. MacFarlane pers. comm. 2008) taken on the mountain slopes ± 3 km NW of Wuppertal on the road to Biedouw Valley on 24 September 2006, also appears to be *M. verecunda*. Plants should be checked at these new localities, which represent the first records of the species in Western Cape and 80 and 100 km from Nieuwoudtville.

WESTERN CAPE.—3219 (Wuppertal): 11 km from Pakhuis Pass to Biedouw Valley, descending down Uitkyk Pass, (–AA), 11 November 1986, *Stirton 11507* (NBG).

Moraea vespertina Goldblatt & J.C.Manning

Described in 2000, based on plants from the dolerite hills east of Nieuwoudtville in Northern Cape, *Moraea vespertina* was distinguished in subgenus *Visciramosa* Goldblatt by its several foliage leaves and relatively large, white flowers opening in the late afternoon and fading shortly after sunset. Subsequently, a second population was reported from Matjiesfontein Farm, lying to the east, between Nieuwoudtville and Calvinia (*Manning s.n.*). The flowers of this population are slightly larger (the outer tepals are ± 45 mm long, filaments 10 mm, anthers 6–7 mm) (Table 2) and on fading become faintly suffused with grey blue. In 2006 and 2007 we collected plants resembling *M. vespertina* in the Tankwa National Park, but with larger, pale grey-blue flowers. At first we considered that they represented a new species, distinguished from *M. vespertina* by the larger perianth, blue-grey coloration, crescent-shaped nectar guide, purple markings and veins on the outer tepal claws and other floral details (Table 2), notably the longer filaments, anthers and style crests. The Tankwa population grows among dolerite boulders on south-trending slopes. Differences between the populations are relatively small and at present we prefer to expand the circumscription of *M. vespertina* rather than to recognize a new taxon. We suspect that more populations of this species remain to be discovered between the Bokkeveld Plateau sites and the Tankwa National Park, over 120 km to the south (Figure

TABLE 2.—Comparison of Nieuwoudtville and Tankwa National Park populations of *Moraea vespertina*. All measurements were taken from fresh material

Character	Nieuwoudtville	Tankwa National Park
Spathe length (mm)	40–45	43–50
Tepal limb length (mm):		
outer	30–32 $\times$ ± 15	30–32 $\times$ ± 20
inner	28–30 $\times$ 8–9	28–30 $\times$ 14–15
Tepal claw length (mm)	10–11	± 16
Perianth colour	white	pale slate-blue, claws purple
Nectar guide shape	longitudinal streak	crescent
Stamens:		
filament length (mm)	7–8	± 12
anther length (mm) and colour	± 6 , linear, white	± 8 , oblong, lilac
Style branches (mm)	7 $\times$ 8	10 $\times$ 9
Style crests length (mm)	± 15	± 20

2) and if so, will no doubt cast more light on questions about the taxonomic status of the southern, larger-flowered population.

The flowers of the Tankwa population opened at 17:00–17:30 and closed at $\pm$ 17:30. When fully open, as the sun began to set, they produced a strong odour of stocks (a heavy, sweet, clove scent). As night fell, we observed settling moths (not captured) visiting the flowers. The strong scent, pale flower colour and timing of anthesis make it all but certain that the Tankwa population is adapted for pollination by settling moths, as was previously reported for the Nieuwoudtville plants (Goldblatt & Manning 2000).

In a curious aside, we report that the corms of *Moraea vespertina* are boiled in goat's milk and eaten locally in the Calvinia District as a delicacy (I. Coetzee pers. comm. 2007). This leads us to think there are more sites for the species, but unfortunately not yet recorded.

NORTHERN CAPE.—3119 (Calvinia): Farm Matjiesfontein between Calvinia and Nieuwoudtville, (–AD), 20 October 2007, Manning s.n. (NBG). 3220 (Sutherland): Tankwa National Park, east end of Elandsberg, (–AA), 16 September 2006, Manning 3060 (NBG); Tankwa National Park, kloof along Maansedam road to Elandsberg, (–AA), 10 September 2007, Goldblatt & Porter 12978 (MO, NBG).

Moraea vlokii Goldblatt

When described (Goldblatt 1992), *Moraea vlokii* was known from two collections in the Swartberg near Gamkakloof at fairly high elevations, one at $\pm$ 985 m and the other at $\pm$ 490 m. We found a third population in 1997 near Montagu, which establishes a wider range for the species and, though still in the Little Karoo, at a lower elevation, below 300 m and some 150 km distant. The species is vegetatively very like the widespread *M. gawleri* Spreng. in corm tunic structure and the unusual, short inflorescence spathes, although it has a single foliage leaf (*M. gawleri* normally has two or three foliage leaves), and Goldblatt postulated that the two were immediately allied. DNA sequence analysis using a single sample of each species shows the two to be sister taxa (Goldblatt *et al.* unpublished data).

WESTERN CAPE.—3320 (Montagu): below Ouberg Pass to Montagu, rock outcrop, $\pm$ 260 m, (–CC), 27 September 1997, Goldblatt & Manning 10764A (MO, NBG).

Moraea sp.

A collection from the summit of the Aurusberg in southwestern Namibia, Williamson & Hamer 4564, NBG, found on 2 November 1992, appears to represent a new species. The flowers, said to be yellow, were destroyed by insects before we received the specimen but it is worthwhile describing the plants for future reference and to establish its existence. Plants appear to grow in tufts in rock crevices on steep south slopes, and have corms $\pm$ 12 mm in diameter and are covered by medium-textured, dark fibres, much like those illustrated for *M. tanquana* (Figure 3). The stems, about 60 mm long, are

unbranched, trailing and bear several, channelled leaves, up to 1 mm wide. The blades are somewhat twisted, have undulate margins and like the stem, they are trailing, but are much longer than the stem. The spathes are almost equal, the inner 13–14 mm long and the outer $\pm$ 12 mm long. Nothing remains of the flowers or buds, but apart from the colour, were said to be *Spiloxene*-like, this with at least partially free filaments and thread-like style branches. We speculate that the flowers were of the *Hexaglottis*-type as illustrated in Figure 1.

ACKNOWLEDGEMENTS

Support for this study by grants 7316-02, 7799-05 and 8248-07 from the National Geographic Society is gratefully acknowledged. We thank Elizabeth Parker and Lendon Porter for assistance and companionship in the field; Jan Vlok for alerting us to the existence of yellow-flowered *Moraea bipartita* and *M. tricolor* at Stilbaai; Ralph Clarke for alerting us to the presence of *M. spathulata* in the Karoo highlands; Tony Dold for providing information about the occurrence of *M. falcifolia* near Alexandria; Janet Naudé for guiding us to populations of *M. tricolor*; Roger MacFarlane for the Wuppertal record of *M. verecunda*; and Sharon Bodine for help with herbarium searches. Roy Gereau kindly checked the Latin descriptions. Collecting permits were provided by the nature conservation authorities of Western Cape and Northern Cape Provinces, South Africa.

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Three new species of *Diascia* (Scrophulariaceae) from the Western Cape, South Africa

K.E. STEINER*

Keywords: *Diascia* Link & Otto, new species, oil-collecting bees, oil-secreting trichomes, Scrophulariaceae, South Africa, Western Cape

ABSTRACT

Three new annual species of *Diascia* Link & Otto are described from the Western Cape Province of South Africa. *D. collina* is characterized by greyish magenta flowers with two divergent yellow sacs containing oil-secreting trichomes. It is restricted to granite outcrops in the vicinity of Saldanha Bay, from the West Coast National Park and Langebaan north to Vredenburg. *D. pusilla* is closely related to *D. collina*, but differs from that species in having smaller flowers with shorter, $\pm$ parallel sacs, and posticous filaments that lack a protuberance where they bend sharply backwards towards the upper lip. It occurs in grey to whitish sands usually near seasonally moist or wet areas. It has not been found more than 35 km from the coast and ranges from Modderivier, south of Darling, north to Lambert's Bay. *D. appendiculata* is related to *D. diffusa* (Thunb.) Benth. and is characterized by having small, mainly reddish lilac to greyish magenta flowers, two shallow depressions in the corolla tube at the base of the upper lip, and posticous filaments with sterile appendages. It is known from only six localities in the general vicinity of Citrusdal and occurs in fynbos vegetation on lower mountain slopes or flats, in loose alluvial sands derived from Table Mountain Sandstone.

INTRODUCTION

Diascia Link & Otto is a genus of $\pm$ 72 species of annual and perennial herbs endemic to southern Africa. Two sections have been recognized, section *Racemosae* with 27 species and section *Diascia* with about 45 species (Hilliard & Burt 1984; Steiner unpubl.). Section *Racemosae* was revised by Hilliard & Burt (1984) and three additional taxa were described more recently (Steiner 1989, 1999). Section *Diascia* has not been revised since Hiern's (1904) treatment in *Flora capensis*, although many new species have been described in recent years as part of a revisionary study (Steiner 1992a, b, c, d 1995). Section *Diascia* consists solely of annual species, whereas section *Racemosae* is mostly perennial (81 %). Three additional new species in Section *Diascia* from the Western Cape are described here. All descriptions are based on living material collected from the field. Flower colours are based on the *Methuen handbook of colour* (Kornerup & Wanscher 1984). Chromosome counts of these species were reported by Steiner (1996).

***Diascia collina* K.E.Steiner, sp. nov., *D. pusillae* K.E.Steiner proxima, sed differt corolla grandiore, sacculis corollae grandioribus divergentibus non parallelis, et filamentis posticis protuberantione instructis.**

TYPE.—Western Cape, 3318 (Cape Town): Postberg Nature Reserve, Vlaeberg loop road, picnic and view site, $\pm$ 200 m, (–AA), 14 Sept. 1988, *Steiner 1816* (NBG, holo.; BOL, E, K, MO, PRE, US, iso.).

Annual herb, rosulate, glabrous, simple or branching from base. *Stems* decumbent, up to 340 mm long, angular, up to 6-sided, ribs 2 or more, sides up to 2 mm wide. *Leaves* simple, alternate, opposite or whorled, petiolate; lamina ovate to obovate, 4–33(–60) $\times$ 3–11(–13) mm, apex rounded to acute or apiculate, base attenuate; mar-

gins lobed to divided, lobes or divisions oblong-ovate to triangular, entire, opposite or subopposite, occasionally alternate, apices rounded to acute or apiculate; petioles up to 37 mm long; cauline leaves progressively smaller upwards. *Flowers* axillary, 1 or 2 open per stem, faintly sweet-scented, nodding in early bud stage; flowering pedicels 20–65 mm long, ascending, dorsiventrally flattened especially where attached to flower, recurving in fruit except for upward curving apical portion. *Calyx* lobes 5, spreading, lanceolate, $\pm$ equal, 3.2–3.6 $\times$ 1.4–1.8 mm, acuminate, the two lower sepals slightly reflexed; margins white-ciliate. *Corolla* bilabiate, 5-lobed, limb 13.3–23.0 $\times$ 14.3–26.0 mm; lobes broadly oblong-obovate, falciform, outer sides longer than inner sides, 4.4–7.1 $\times$ 5.2–5.7(–7.9) mm, apices rounded, bases oblique; lateral lobes broadly obovate, emarginate, 5.4–7.1 $\times$ 5.2–6.8 (–8.3) mm, sides $\pm$ equal; lower lobe obcordate, 6.2–9.7 $\times$ 5.4–8.1(–11.4); upper lobes greyish magenta (14D6) with deep magenta veins or lines at base; other lobes similar in colour but without veining, all with scattered, dark purple, peltate glandular trichomes, especially on inner surface near base; tube shallowly cupped, deep magenta; bisaccate, sacs oblong-ovate, rounded, 4–5 $\times$ 2.0–2.5 mm, mostly yellow, widely diverging, oil-secreting glandular trichomes within; central, stamen-bearing boss oblique, anticous portion 1.1–1.5 mm high, deep magenta, posticous portion 0.3–0.6 mm high, yellow. *Stamens* 4, erect, partly hidden; anticous filaments (twisted at base and appearing posticous) falciform, $\pm$ 3.4–3.6 mm long, bases strongly curved, pubescent, trichomes clavate, purple; posticous filaments geniculate, thickened, 1.9–2.0 mm long, bend with protuberance $\pm$ 1 mm from base, pubescent, trichomes clavate, purple; anthers $\pm$ 0.50–0.80 mm, strongly cohering, grey; pollen orange (fading to yellow in pressed specimens). *Ovary* oblong-ovoid, laterally compressed contrary to septum, 1.6–1.7 $\times$ 1 mm; style $\pm$ 1.6–2.0 mm long, reddish purple, curving forward in distal third; stigma capitate, surrounded by anthers; ovules $\pm$ 35–45. *Capsule* ovoid to oblong-ovoid, 5.1–8.1 $\times$ 3.3–5.8 mm, exceeding sepals at maturity, base oblique. *Seeds* reniform, 1.0–1.2 mm long, dorsal surface ridged, ventral surface with an oblong keyhole-like

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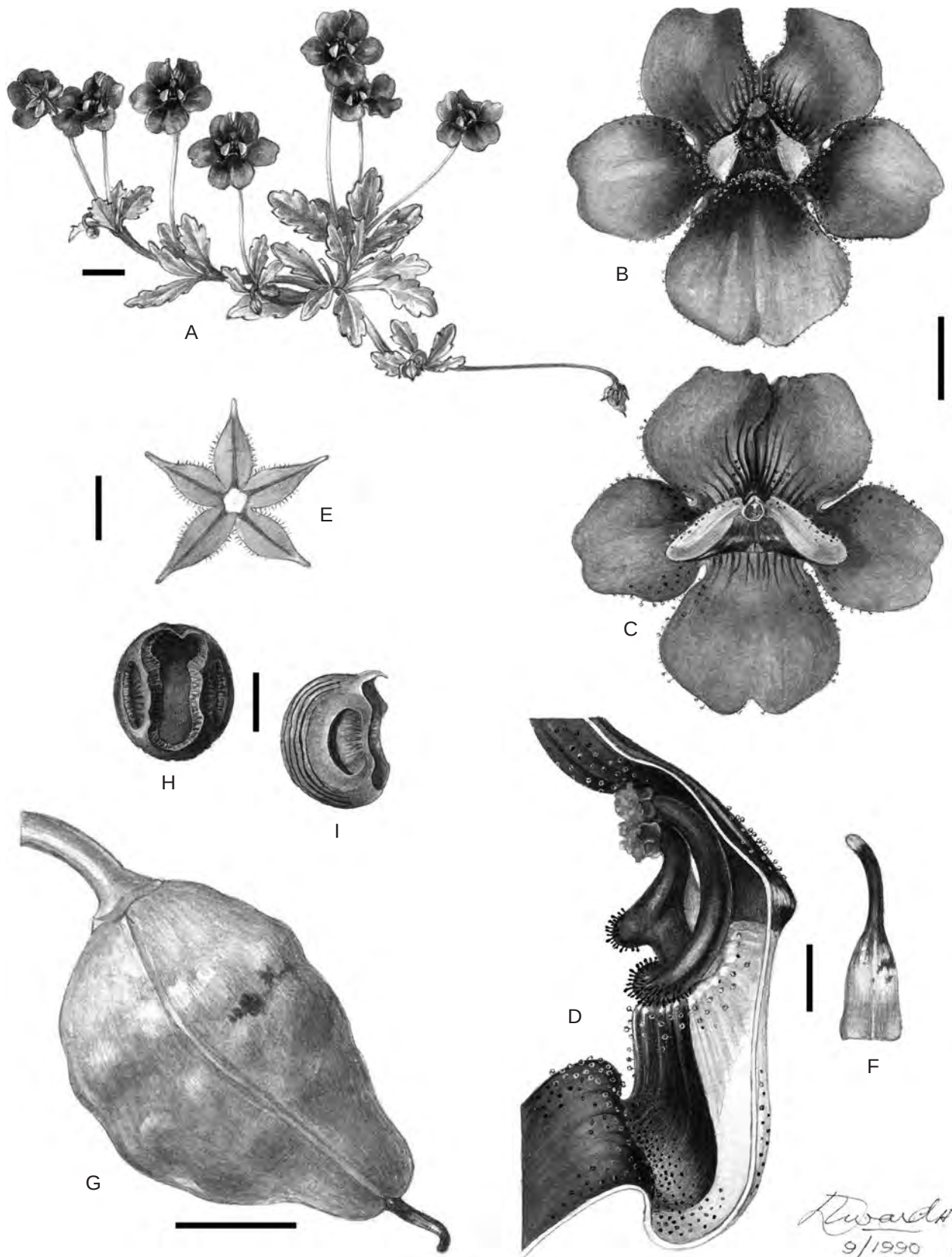


FIGURE 1.—*Diascia collina*, Steiner 2219 (NBG). A, habit. B–D, flower: B, C, front and rear views; D, side view partially cut away. E, calyx; F, pistil; G, capsule. H, I, seed: H, ventral view; I, side view. Scale bars: A, 10 mm; B, C, 4 mm; D, E, 1 mm; F, 3 mm; G, 2 mm; H, I, 0.5 mm. Artist: Ellaphie Ward-Hillhorst.

opening formed by extensions of seed coat, long sides of opening bearing a reniform perforation; embryo curved. Chromosome no.: $2n = 18$. Flowering time: August–September. Figure 1.

Diagnostic features: *Diascia collina* is most similar to *D. pusilla*, but it differs from that species in having a larger corolla ($13.3\text{--}23.0 \times 14.3\text{--}26.0$ mm vs $9.1\text{--}13.5 \times 9.0\text{--}14.3$ mm), longer corolla sacs ($4\text{--}5$ mm vs 2.2--

2.5 mm long) and a protuberance from the posticous filaments where they bend backwards (Figure 1). *D. collina* is also similar to *D. capensis* (L.) Britten, but differs from that species in having stamens that are $\pm$ half the size and backwards-bending, rather than forward-arching. *D. collina* also has a shorter style (1.3–2.0 mm vs 3.5–5.2 mm) that is less curved, and corolla sacs that are strongly divergent, not $\pm$ parallel like those of *D. capensis*.

Etymology: the name refers to the hills of granite where the species occurs.

Distribution and habitat: *Diascia collina* is known only from the Postberg section of the West Coast National Park, from undeveloped areas in and around the town of Langebaan directly across the lagoon from Postberg, and from the granite outcrops on the southern edge of Vredenburg (Figure 2). It ranges in elevation from near sea level to about 200 m. In Postberg, *D. collina* is fairly common around the Uitkyk picnic area on Vlaeberg ridge overlooking Langebaan Lagoon. It has also been seen near the entrance to the SADF restricted area at the northwest end of the Postberg Reserve. *D. collina* occurs under and around medium to large shrubs and can be considered endemic to Saldanha Granite Strandveld vegetation (Mucina & Rutherford 2006). In Langebaan and Vredenburg, this habitat is quickly disappearing due to residential expansion.

Pollination and breeding system: based on observations of cultivated plants, *Diascia collina* is self-incompatible and, at Postberg, it is pollinated by two species of oil-collecting bees, *Rediviva peringueyi* Friese and *R. aurata* Whitehead & Steiner (Melittidae) (Whitehead & Steiner 2001). These bees use the specially modified setae on their forelegs to collect oil from the paired yellow corolla sacs. The pollen is deposited on the frons or face of the pollinating bees.

Other specimens examined

WESTERN CAPE.—3217 (Saldanha): Vredenburg, new housing development at Witklip near old granite quarry (S32° 55.228' E17° 58.700'), $\pm$ 150 m, (–DD), 16 Sept. 2004, Steiner 4101 (CAS); *ibid.*, 2 Sept. 2005, Steiner 4121 (CAS, K, NBG, PRE, US). 3318 (Cape Town): Postberg Nature Reserve, Vlaeberg loop road, picnic and view site, (–AA), 5 Sept. 1990, Steiner 2219 (NBG). Langebaan Hill, sandy slopes, (–AA), 24 Aug. 1995, Goldblatt & Manning 10280 (NBG); *ibid.*, 25 Sept. 1995, Goldblatt & Manning 10321 (NBG); Langebaan, rocky outcrop near town, (–AA), 23 Aug. 1998, Goldblatt & Manning 10994 (NBG); Langebaan hills, above town, in vacant lot opposite 82 Sunbird Lane (S 33°06.172' E 18°02.574'), $\pm$ 18 m, (–AA), 30 Aug. 2001, Steiner 3697 (NBG, CAS); Langebaan, between day care centre and Pikkieland fun park, (S33°05.461' E18°02.207'), $\pm$ 5 m, (–AA), 6 Sept. 2002, Steiner 3870 (NBG, CAS).

***Diascia pusilla* K.E.Steiner, sp. nov., *D. collinae* K.E.Steiner proxima, sed differt corolla brevior, sacculis corollae parallelis non divergentibus et filamentis posticis sine protuberantibus.**

TYPE.—Western Cape, 3218 (Clanwilliam): Farm Droogerivier, road 365, 8.6 km N of turnoff to Alexandershoek, $\pm$ 200 m west of road, (–BC), 16 Sept. 1988, Steiner 1819 (NBG, holo.; K, MO, PRE, iso.).

Annual herb, rosulate, glabrous, simple or branching from base. Stems decumbent, up to 150 mm long,

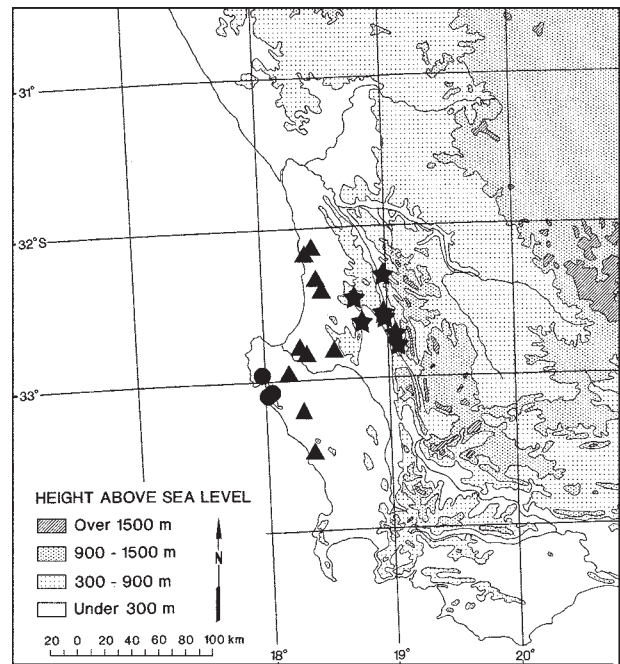


FIGURE 2.—Known distributions of *Diascia collina*, ●; *D. pusilla*, ▲; and *D. appendiculata*, ★.

angular, up to 6-sided, ribs 2 or more, sides up to 2 mm wide. Leaves simple, opposite or alternate, petiolate; lamina obovate to elliptic, 5–28 $\times$ 2–9 mm, apex acute to apiculate, base attenuate; margins lobed to divided, lobes or divisions ovate to triangular, entire, acute to apiculate; petioles up to $\pm$ 12 mm long; cauline leaves progressively smaller upwards. Flowers axillary, 1 to 3 open per branch, unscented; pedicels 17–23 mm long, ascending, dorsiventrally flattened especially where attached to flower, recurved in fruit except for upward curving apical portion. Calyx lobes 5, spreading, lanceolate, $\pm$ equal, 2.3–2.9 $\times$ 1.0–1.2 mm, acuminate; margins white-ciliate. Corolla bilabiate, 5-lobed, limb 9.1–13.5 $\times$ 9.0–14.3 mm; lobes broadly ovate; upper lobes 2.6–3.5 $\times$ 2.9–4.0 mm, outer sides longer than inner sides, apices rounded to emarginate, bases oblique; lateral lobes 2.5–3.5 $\times$ 3.0–3.5 mm, sides $\pm$ equal, apices rounded; lower lobe 3.3–5.0 $\times$ 3.2–5.8 mm, emarginate to obcordate; upper lobes greyish magenta (14D6) on inner surface, pinkish white (13A2) on reverse side, with deep magenta (14E8) lines at base; other lobes similar in colour but lacking lines, sparsely glandular puberulous with dark violet, glandular trichomes, especially on inner surface near base; tube shallowly cupped, deep magenta and yellow, bisaccate, sacs ovate in outline, 2.2–2.5 $\times$ 1.2–1.4 mm, projecting downward and diverging slightly at tips, yellow, oil-secreting glandular trichomes within; central stamen-bearing boss oblique, anticous portion 1.2–1.9 mm high, deep magenta (14E8), posticous portion 0.3–0.5 mm high, yellow. Stamens 4, erect, partly hidden; anticous filaments (twisted at base and appearing posticous) falciform, 3.0–3.2 mm long, bases strongly curved, sparsely pubescent, trichomes clavate; posticous filaments geniculate, thickened, 2.0–2.5 mm long, bend pubescent, trichomes clavate, dark violet, apical portions, below anthers, bent forward without enlargement; all filaments greyish magenta (13E6) except

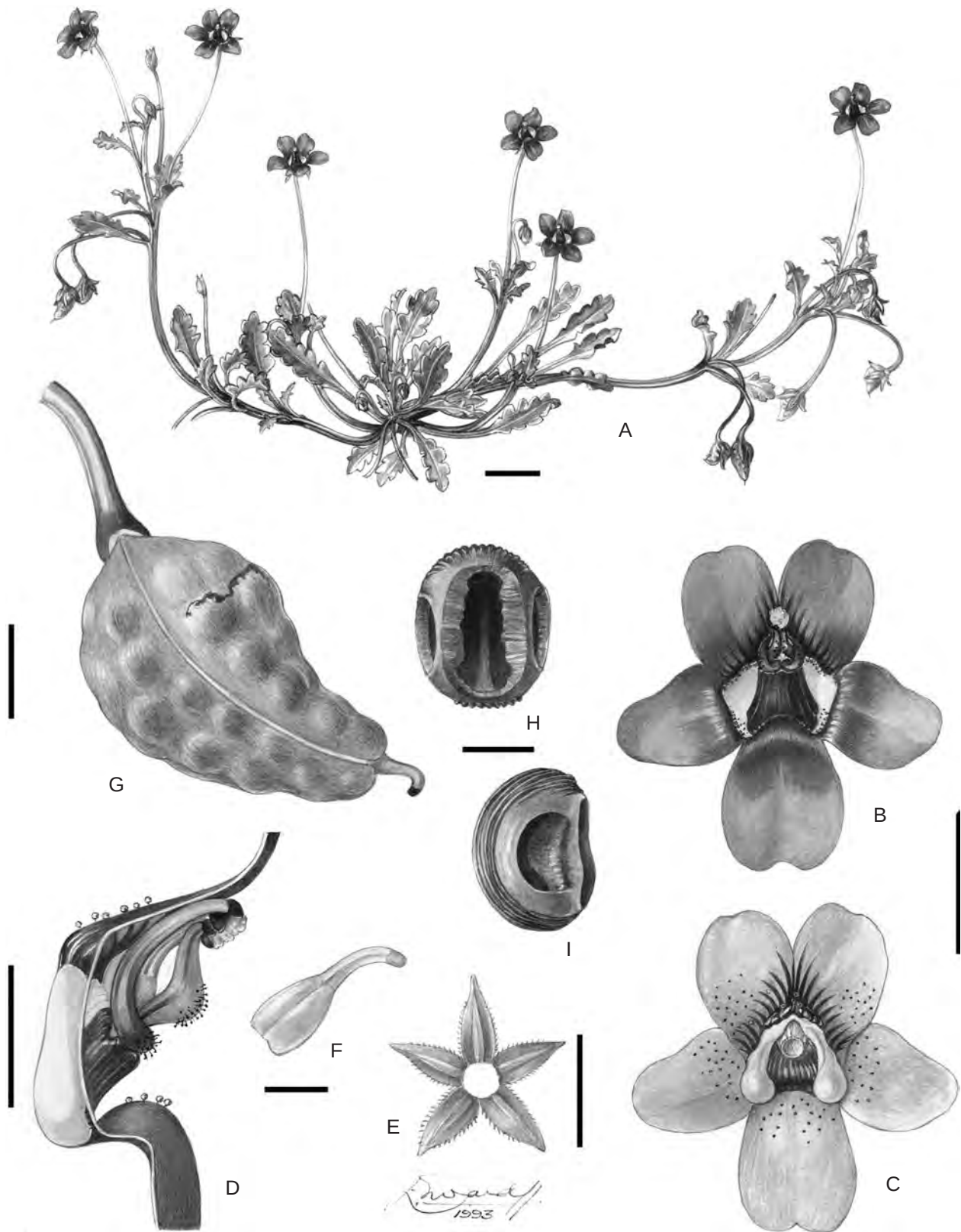


FIGURE 3.—*Diascia pusilla*, Steiner 1819 (NBG). A, habit. B–D, flower: B, C, front and rear views; D, side view partially cut away. E, calyx; F, pistil; G, capsule. H, I, seed: H, ventral view; I, side view. Scale bars: A, 10 mm; B, C, 5 mm; D, 2 mm; E, 3 mm; F, 1 mm; G, 2 mm; H, I, 0.5 mm. Artist: Ellaphie Ward-Hilhorst.

just below anthers; anthers 0.3–0.5 mm long, strongly cohering, grey; pollen yellow to orange. *Ovary* oblong-ovoid, laterally compressed contrary to septum, 1.2–1.5 × 0.9–1.0 mm; style 1.3–1.5 mm long, curving forward at tip; stigma subcapitate, surrounded by anthers;

ovules ± 23–38. *Capsule* falciform ovoid, 6.0–7.1 × 3.5–4.6 mm, ± twice as long as calyx at maturity. *Seeds* reniform, 0.9–1.2 mm long, dorsal surface ridged, ventral surface with an oblong, keyhole-like opening formed by extensions of seed coat, long sides of open-

ing bearing a reniform perforation; embryo curved. *Chromosome no.*: $2n = 18$. *Flowering time*: August–September. Figure 3.

Diagnostic features: *Diascia pusilla* differs from its nearest relative, *D. collina*, in corolla size, shape of the posticous filaments, size and shape of the corolla sacs, and habitat. The difference in flower size between the two taxa is not simply a function of plant vigour, since small plants of *D. collina* at Postberg, with only a few leaves, have much larger flowers than robust plants of *D. pusilla*, with many large leaves and long thick stems, at Droogerivier. Corolla limb length of *D. pusilla* reaches 13.5 mm, but averages 11.5 mm, whereas limb length of *D. collina* ranges from 13.3 to 23 mm, but averages 17 mm. The corolla sacs of *D. pusilla* are about half the size of *D. collina* sacs (2.1 mm vs 4.4 mm long) and are parallel or only slightly divergent near the tips. They are not strongly divergent like those of *D. collina*. The shapes of the filaments also differ between these two species. *D. pusilla* lacks the protuberance on each posticous filament that is present in *D. collina*.

Etymology: the name refers to the small size of the flowers.

Distribution and habitat: *Diascia pusilla* is known from a narrow strip along the Cape west coast, from the Farm Modderivier (Mud River) (southwest of Darling), north to Lambert's Bay and as far east as Droogerivier (± 4.5 km SE of Sandberg). It occurs no more than 35 km from the sea and ranges in elevation from sea level to nearly 100 m (Figure 2). On the farms Droogerivier and Suurfontein (near Lambert's Bay), it occurs in or near riverine or vlei systems, often in poorly drained, seasonally wet sands, but in other localities, the habitat is drier. In all cases, it occurs in loose white to greyish sands. Southwest of Darling it has been reported from short fynbos in deep sand (*Hugo 2427*). It does not occur in areas with granitic outcrops, typical of *D. collina*.

Pollination and breeding system: like most *Diascia* species, *D. pusilla* has oil-secreting glands in its corolla sacs. Unlike *D. collina*, this species is facultatively autogamous and, therefore, does not need visits by oil-collecting bees to set seed. At the type locality, and at least one other locality, *D. pusilla* occurs and flowers concurrently with *Hemimeris racemosa* (Scrophulariaceae), another oil-secreting species. Since at both these sites oil-collecting bees have been caught on *H. racemosa*, it is probable that these same bees visit *D. pusilla*. At the type locality, Droogerivier, and at Kersefontein, *D. pusilla* occurs with *Rediviva parva* (Whitehead & Steiner 2001).

Other specimens examined

WESTERN CAPE.—3218 (Clanwilliam): Farm Suurfontein (± 13 km E of Lambert's Bay), 6.8 km E of turnoff to Doringbaai ($S32^{\circ}07'20.9''$ $E18^{\circ}25'71.0''$), ± 50 m, (–AB), 4 Sept. 2001, Steiner 3718 (CAS, NBG); Farm Wagendrift, 12.1 km S of Lambert's Bay, ± 5 m, (–AB), 12 Sept. 1991, Steiner 2386 (NBG); Elandsbaai–Redelinghuys rd, 8.9 km NW of Redelinghuys turnoff, ± 40 m, (–AD), 14 Sept. 1984, Steiner 775 (NBG); *ibid.*, 19 Sept. 1988, Steiner 1822 (NBG); Farm Droogerivier, Road 365, 8.6 km N of turnoff to Alexandershoek, ± 200 m west of road, (–BC), 14 Aug. 1987, Steiner 1570 (NBG); *ibid.*, 19 Aug. 1993, Steiner 2663 (NBG); Langebaanweg, (–CC), 13 Sept. 1991, Goldblatt & Manning 9207 (NBG); Farm Kersefontein, 5.9 km N of

Berg River, ± 20 m, (–CD), 17 Sept. 1991, Whitehead 1 (NBG); Farm Doornfontein A, ± 30 m, (–CD), 9 Sept. 1994, Steiner 2886 (NBG); Farm Suurfontein, 0.7 km W of Sauer Post Office, ± 30 m, (–DC), 10 Sept. 1990, Steiner 2226 (NBG). 3318 (Cape Town): Farm Baarhuis (NW of Darling), 0.5 km N of entrance to Farm Skilpadfontein, ($S33^{\circ}14.769'$ $E18^{\circ}18.334'$), ± 65 m, (–AB), 16 Sept. 2005, Steiner 4168 (CAS, NBG); Farm Modderivier, southwest of Darling along new National Road, ± 80 m, (–AD), July 1980, *Hugo 2427* (PRE).

***Diascia appendiculata* K.E.Steiner, sp. nov., *D. diffusae* (Thunb.) Benth. proxima**, sed differt floribus brevioribus, sacculis corollae destituti, staminibus erectis nec patentibus et filamentis glabris.

TYPE.—Western Cape, 3218 (Clanwilliam): Grey's Pass (Modderfontein), 4.2 km N of turnoff to Paleisheuwel, ± 290 m, (–DB), 9 Sept. 1989, Steiner 1978 (NBG, *holo.*; CAS, K, MO, PRE, US, *iso.*).

Annual herb, rosulate, glabrous, simple or branching from base. *Stems* decumbent, up to 220 mm long, angular, up to 6-sided, ribs 2 or more, sides up to 2 mm wide. *Leaves* simple, alternate, opposite or whorled, petiolate, erect or spreading; lamina mostly oblong, but also ovate to obovate, $9\text{--}35 \times 3\text{--}9$ mm, apex acute to rounded, base attenuate; margins sinuate, pinnatipartite or pinnatisect, lobes up to ± 5 mm long, ovate, obovate, oblong or deltoid, apices rounded to acute; petioles up to ± 15 mm long; cauline leaves progressively smaller upwards. *Flowers* axillary, 1 or 2 open flowers per stem, nodding in bud, long pedicelate; pedicels 17–53 mm long, ascending, dorsiventrally flattened especially where attached to flower, elongating and spreading at right angles to stem in fruit, with an abrupt downward curve 3–4 mm from base of developing capsule. *Calyx* lobes 5, spreading, lanceolate, acuminate, margins white-ciliate, upper 3 segments $\pm$ equal, $2.4\text{--}3.1 \times 1.0\text{--}1.6$ mm, lower 2 segments slightly wider. *Corolla* bilabiate, 5-lobed, limb $7.4\text{--}14.3 \times 7.7\text{--}14.8$ mm; upper lobes ovate to obovate, $2.0\text{--}4.7 \times 2.5\text{--}5.2$ mm, outer sides longer than inner sides, apices rounded to emarginate, bases oblique; lateral lobes oblong-ovate, $2.5\text{--}4.6 \times 2.8\text{--}4.6$ mm, sides $\pm$ equal in length, apices rounded to emarginate, lower lobe obcordate, $3.1\text{--}5.0 \times 3.6\text{--}6.4$ mm, all lobes reddish lilac (14C4) to greyish magenta (14D6) on inner surface and violet-white to purplish white on reverse side, with scattered black or clear glandular trichomes on both sides; tube shallowly cupped, dark ruby to violet-brown, very shallowly bisaccate, sacs or depressions $0.3\text{--}1.0 \times 1.0\text{--}1.6$ mm, $0.5\text{--}0.7$ mm deep, yellow, oil-secreting trichomes clustered within; central stamen-bearing boss oblique, sparsely glandular pubescent, anticous portion $0.5\text{--}1.0$ mm high, ruby, posticous portion ± 2.0 mm high, yellow. *Stamens* 4, erect from the boss; filaments ruby, usually glabrous, occasionally covered with dark purple, clavate trichomes; anticous filaments (twisted at the base and appearing posticous) $\pm$ straight, $2.1\text{--}2.5$ mm long, base strongly curved; posticous filaments ± 2.3 mm long, with sterile appendages, ± 0.8 mm from base, appendages $0.1\text{--}0.8$ mm long, sometimes reduced in length to a small nub, filament above bend ± 1.5 mm long; anthers 0.3 mm long, strongly cohering, greenish yellow; pollen orange. *Ovary* ovoid, laterally compressed contrary to septum, $1.2\text{--}1.5 \times 0.8\text{--}1.1$ mm, falciform; ovules 27–47; style ± 1.2 mm long,

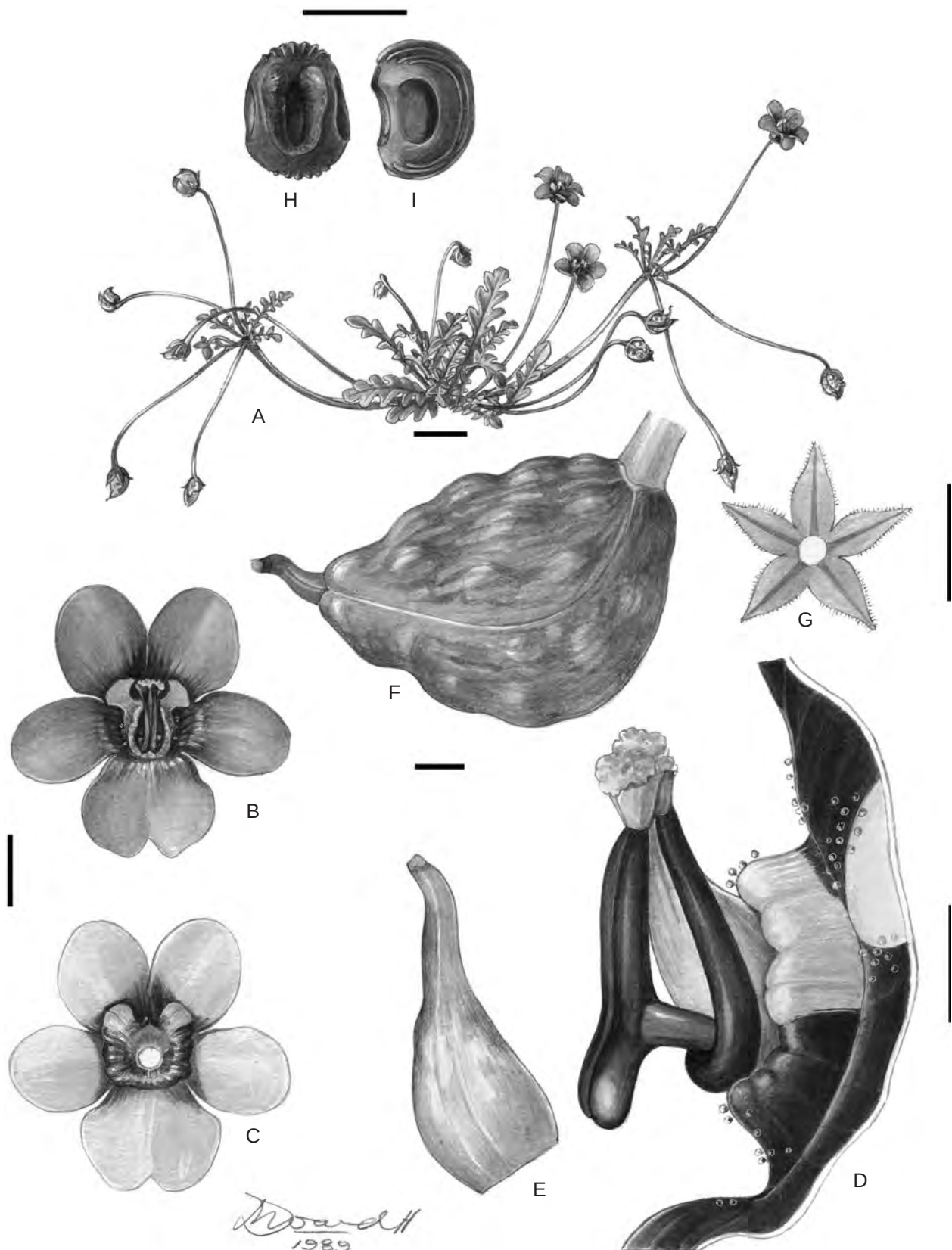


FIGURE 4.—*Diascia appendiculata*, Steiner 1978 (NBG). A, habit. B–D, flower: B, C, front and rear views; D, side view partially cut away. E, pistil; F, capsule; G, calyx. H, I, seed: H, ventral view; I, side view. Scale bars: A, 10 mm; B, C, 3 mm; D, E, 1 mm; F, 1 mm; G, 4 mm; H, I, 1 mm. Artist: Ellaphie Ward-Hilhorst.

deflected upwards, $\pm$ straight or curved forward near tip; stigma capitate, surrounded by anthers or emerging slightly. *Capsule* falciform ovoid, $(5.0\text{--})6.4\text{--}7.5 \times (2.5\text{--})4.0\text{--}5.0$ mm, about twice as long as calyx at maturity, base

oblique, often resting on soil surface during development with pedicel ascending just before dehiscence. *Seeds* reniform, 1.3–1.5 mm long, dorsal surface with parallel ridges, ventral surface with oblong keyhole-like opening formed

by extensions of seed coat, long sides of opening bearing reniform perforation; embryo curved. *Chromosome no.*: $2n = 18$. *Flowering time*: August–September.

Diagnostic features: *Diascia appendiculata* is most closely allied to *D. diffusa*. Both species have posticous filaments with sterile appendages, but the stamens are erect in *D. appendiculata* and projecting forward in *D. diffusa*. Furthermore, the filaments in *D. appendiculata* are usually glabrous, whereas those of *D. diffusa* have clavate trichomes. Both species also have two localized patches of oil-secreting trichomes, but in *D. diffusa* they are clustered in two short, but distinct, spurs (at the base of the upper corolla lip), whereas in *D. appendiculata* they are present in two shallow, yellow depressions that may or may not be visible on the outside of the corolla as a slight swelling of the tube.

Etymology: the name refers to the filament appendages.

Distribution and habitat: *Diascia appendiculata* is known from only six localities in the general vicinity of Citrusdal (Figure 2). It occurs between elevations of 100 to 300 m in fynbos vegetation on lower mountain slopes or flats in loose alluvial sands derived from Table Mountain Sandstone. In five of the localities it occurred on first year burns, while in the other locality it was collected from a roadside area next to cultivated land at the northeastern base of the Piketberg. On Grey's Pass, it was most abundant in the first season after fire, but was also observed in the second and third years (1990, 1991) after fire. It could not be found in the fifth and sixth years. The stimulation of germination in response to fire is also found in other *Diascia* species such as *D. elongata* Benth. and *D. maculata* K.E.Steiner.

Pollination and breeding system: *Diascia appendiculata* is facultatively autogamous. However, because it secretes floral oil, it is probably visited and cross-pollinated, at least occasionally, by small oil-collecting *Rediviva* bees (Melittidae) such as *R. parva* Whitehead & Steiner, *R. intermixta* (Cockerell) or *R. aurata* Whitehead & Steiner (Whitehead & Steiner 2001).

Other specimens examined

WESTERN CAPE.—3218 (Clanwilliam): Farm Swartboskraal, 6.7 km N of turnoff to Citrusdal on Paleisheuvel–Sandberg road, 270 m, (–BC), 22 Aug. 1991, *Steiner* 2334 (NBG); *ibid.* 1.5 km S of farm entrance, 218 m, (–BC), 31 Aug. 2004, *Steiner* 4082 (NBG); Farm Kriebberg, 7.2 km E of old Clanwilliam–Citrusdal road on road to Algeria, $\pm$ 290 m, (–BD), 16 Sept. 1989, *Steiner* 2009 (NBG); *ibid.*, 24 Sept. 1989, *Steiner* 2025 (NBG); N7, 1.6 km N of turnoff to Citrusdal,

$\pm$ 280 m, (–DB), 10 Aug. 1998, *Steiner* 3287 (NBG); Farm Kanarieberg, Road 366, 5.7 km S of junction with Road 365 to Lambert's Bay, $\pm$ 110 m, (–DB), 21 Sept. 1984, *Steiner* 776 (NBG). 3219 (Wuppertal): Farm Moddervlei, 13.6 km south of Citrusdal on road to Keerom, $\pm$ 210 m, (–CA), 6 Sept. 1991, *Steiner* 2357 (NBG); Farm Karmmelksvlei, 19.6 km south of Citrusdal on road to Keerom, $\pm$ 250 m, (–CC), 6 Sept. 1991, *Steiner* 2362 (NBG).

ACKNOWLEDGEMENTS

I thank Western Cape Nature Conservation and the Western Cape National Park (formerly Postberg Wildflower Reserve) for permission to collect in areas under their jurisdiction. I thank SANBI for the loan of specimens from NBG and PRE and for permission to use the illustrations by E. Ward-Hilhorst. I also thank the Compton Herbarium for the use of their facilities and S. Smithies and T. Arnold for helpful comments on the manuscript.

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Aloe in Angola (Asphodelaceae: Alooiidae)

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Keywords: *Aloe* L., Angola, Asphodelaceae, flora

ABSTRACT

Botanical exploration of Angola was virtually impossible during the almost three-decade-long civil war. With more areas becoming accessible, there is, however, a revived interest in the flora of this country. A total of 27 members of the genus *Aloe* L. have been recorded for Angola. It is not unlikely that new taxa will be discovered, and that the distribution ranges of others will be expanded now that botanical exploration in Angola has resumed. This manuscript provides a complete taxonomic treatment of the known *Aloe* taxa in Angola. It includes, amongst other information, identification keys, descriptions and distribution maps.

INTRODUCTION

The Republic of Angola covers an area of $\pm 1\,246\,700\text{ km}^2$ in southwest-central Africa. Its western boundary is 1 650 km along the Atlantic Ocean and it is bordered by Namibia in the south, the Democratic Republic of Congo in the north and northeast, and Zambia in the east. The detached province of Cabinda has a border with the Republic of Congo in the north and the Democratic Republic of the Congo in the southeast (<http://www.angola.org>) (Figure 1).

The geography of Angola is extremely varied. The flat coastal part has a few shallow bays and is bordered by a sparsely vegetated coastal plain that extends inland for 48–165 km. This coastal belt is separated from the central plateau by an intermediate mountain belt of irregular terraces, running mostly parallel to the coast. Water is more abundant in these mountain chains and the vegetation is therefore lush. The central plateau has an altitude of 1 200–1 800 m and consists of rolling plains and low hills with scanty vegetation. The plateau falls away in the east to the basins of the Congo and Zambezi Rivers and merges with the barren, sandy Namib Desert in the south. Several small rivers arise in the mountain belt and drain westward to the sea. The largest of these are the Cuanza and Cunene Rivers. From the plateau, the Cuango and other rivers flow northwards to join the Casai River, one of the largest tributaries of the Congo River. Rivers in the south of the country either belong to the Zambezi River system or, like the Okavango, drain to Lake Ngami in Botswana (http://www.biocrawler.com/encyclopedia/Geography_of_Angola).

Angola is situated in a subtropical zone, but owing to several factors, the climate of the country is not typical of such areas. Angola's climate is influenced by the cold Benguela Current along the southern part of the coast, the highlands in the interior and the Namib Desert in the southwest.

The country has two distinct seasons: the rainy season from October to May, with average coastal temperatures of around 21°C and the dryer season with lower average coastal temperatures of around 16°C and mist or *Cacimbo* from June to September. The heaviest rains occur in April and are accompanied by violent storms. Rainfall along the coast is high and gradually decreases from 800 mm in the north to 50 mm in the south. The interior can be divided into three zones: the North, with very heavy rains and high temperatures; the Central Plateau, a dry area with average temperatures; and the South with temperature fluctuations due to the proximity of the Kalahari Desert and the influence of tropical air currents (http://www.biocrawler.com/encyclopedia/Geography_of_Angola).

The vegetation of Angola is predominantly Zambezan and falls mainly within the Tropical Grassland (Savanna) zone. Six of White's phytochoria are represented in the country (White 1983). Humid tropical rainforest occurs in the north of the country and the arid Namib Desert and Karoo-Namib shrubland occur in a narrow coastal strip in the southwest. Elsewhere the vegetation consists mostly of miombo woodland, dry evergreen forest, dry deciduous forest, grassland and savanna with Afromontane formations in the highlands (Airy Shaw 1947; Costa *et al.* 2004). In a recent classification of terrestrial ecoregions based on ecological features, climate, and plant and animal communities, 15 regions are represented in Angola (World Wildlife Fund 2001).

The geography and unique climatic characteristics of the area provide Angola with a rich biodiversity. However, the flora of the country remains poorly known, a situation recently addressed by Figueiredo & Smith (2008). Although the first botanical specimens from Angola were collected towards the end of the 18th century and various explorations were carried out during the 18th, 19th and 20th centuries, the Angolan Civil War (1975–2002) prevented the country from being properly surveyed for almost three decades. After the end of the civil war, some areas are still inaccessible owing to the threat of landmines (Costa *et al.* 2004). Even before the war, the poor condition of some roads prevented explorers from reaching many isolated habitats in this country. This situation still prevails to some extent today. With certain areas of the country becoming increasingly accessible, a new interest in the botanical wealth of Angola is surfacing.

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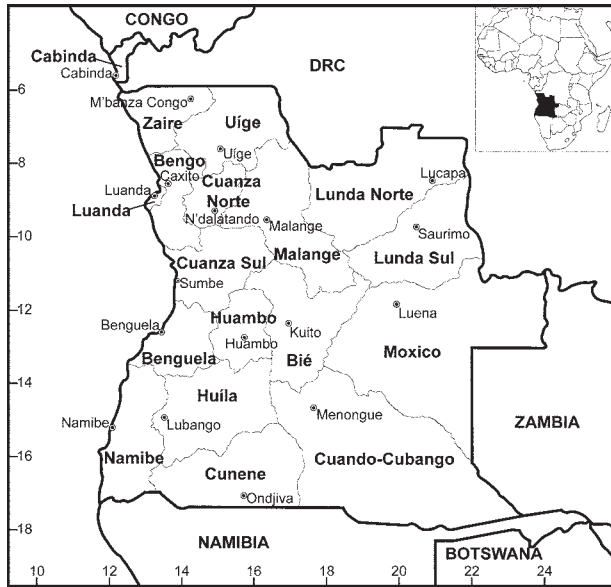


FIGURE 1.—Map of Angola showing the provinces.

In 2006, a project on the flora of Angola, Flora of Angola Online (FLAN) was initiated in the South African National Biodiversity Institute (SANBI), with the collaboration of the Instituto de Investigação Científica Tropical in Lisbon, Portugal, and the Instituto de Investigação Agronómica in Angola. The project had the objective of producing a compilation of plant names with associated specimen data, with the collaboration of 32 botanists. As a result of this joint effort, a comprehensive list of the vascular plants of Angola was compiled (Figueiredo & Smith 2008).

The results of that project (Figueiredo & Smith 2008; Figueiredo *et al.* in press) provide the following data for the plant diversity of the country: a total vascular flora of 7 296 taxa, consisting of 6 961 species (of which 6 735 are indigenous) and 335 infraspecific taxa (of which 331 are indigenous), belonging to 250 families; 997 species and 72 infraspecific taxa are endemic.

This manuscript provides a complete treatment of the known *Aloe* L. taxa in Angola. It is the culmination of research done for the Angolan Flora Project and also forms part of the Aloes of the World Project, which is funded by the Andrew W. Mellon Foundation. Its objectives are to compile as much information as possible on representatives of the genus *Aloe* and to make this data available to a broad range of stakeholders through the internet as part of the African Plants Initiative of Aluka (Smith *et al.* 2008a, b).

MATERIALS AND METHODS

Geo-referencing of specimens was undertaken for all the specimens examined. The co-ordinates of the collecting locality of each specimen were determined using the Angolan map collection kept at the Instituto de Investigação Científica Tropical. Distribution maps are based on the type specimens and those cited under *Additional specimens examined*. These specimens are mainly housed in LISC and PRE, but also in BM, BR, E, G, K, LISU, M and MO (acronyms as in Holmgren *et*

al. 1990). Specimens not housed at LISC, LISU or PRE were viewed on the Aluka website (<http://www.aluka.org>) of the African Plants Initiative. Specimens housed at B were viewed on the virtual herbarium website of the Herbarium Barolinense (Röpert 2000). Further distribution records for taxa with a distribution range extending outside Angola, were obtained from specimens cited in treatments of the genus in *Flora zambesiaca* (Carter 2001) and *Flora of tropical East Africa* (Carter 1994), as well as specimens housed at PRE.

This treatment includes a summary of the discovery of aloes in Angola, as well as identification keys to the taxa using either field or herbarium characters. For each taxon a description, based on the abbreviated description template of the Aloes of the World Project (Smith *et al.* 2008a, b), is provided. Other information that is supplied for each taxon includes the protologue citation, type specimen information, diagnostic characters and specimens investigated, as well as notes on habitat, flowering time, distribution and endemism (indicated by ^E in front of the taxon name). Each taxon is further accompanied by a distribution map.

HISTORY OF ALOE DISCOVERY IN ANGOLA

The known *Aloe* taxa in Angola currently number 27, of which at least 16 (59 %) are endemic to the country. Only five of the 27 Angolan aloes (*A. bulbicaulis* Christian, *A. christianii* Reynolds, *A. dinteri* A. Berger, *A. hereroensis* Engl. and *A. nuttii* Baker) do not have their type localities within Angola. The other 22 *Aloe* taxa occurring in the country were described from material collected during plant collecting surveys or expeditions to Angola from the mid-1800s up to as recently as 1973. Important collectors of *Aloe* in Angola were Dr Friedrich Welwitsch (1853–1861), Lieut. Wissmann & P. Pogge during their expedition through Angola and the Democratic Republic of Congo (1881–1882), Hugo Baum during the Kunene-Zambezi Expedition (1899–1900), John Gossweiler (1903–1944), Edgar Milne-Redhead (1938), Eduardo J. Mendes (1955–1956 and 1959–1960), Gilbert W. Reynolds (1959), Larry C. Leach & I. C. Cannell during the early 1970s and Baptista de Sousa (1973). Botanical exploration and the possible discovery of new *Aloe* taxa ceased with the advent of the 27-year-long Angolan Civil War. As a result of vast areas of the country remaining unexplored, it is likely that more taxa will be found once detailed botanical surveys of these areas are resumed.

The first *Aloe* specimens from Angola were collected by Welwitsch during 1853–1861. From these collections Baker (1878) described six new species, of which only *A. platyphylla* Baker was later reduced to synonymy under *A. zebrina* Baker, and *A. angolensis* Baker is sometimes considered to be either a hybrid between *A. zebrina* and *A. littoralis* Baker or to be a synonym of the latter species (Glen & Hardy 2000; Carter 2001). A further species, *A. venenosa* Engl., was described by Engler (1893) from material collected by Wissmann & Pogge during their expedition through Angola and the Democratic Republic of Congo in 1881–1882. This species has not been collected since and remains insufficiently known. During the Kunene-Zambezi Expedition

of 1899 to 1900, Baum collected *Aloe* specimens from which three new species were described by Engler & Gilg (1903). However, only *A. metallica* Engl. & Gilg is still regarded as a valid species, whereas *A. brunneo-punctata* Engl. & Gilg and *A. baumii* Engl. & Gilg have been reduced to synonymy under *A. nuttii* Baker and *A. zebrina*, respectively.

In 1903, Gossweiler collected material that was later described by Berger (1906) as *Aloe paedogona* A.Berger. Christian (1936) described *A. bulbicaulis* Christian from material collected by Porter in Zambia, but Reynolds (1966) later established that it is a later synonym of *A. paedogona*. The latter species is, furthermore, considered by some (Reynolds 1966; Keay 1968) as a synonym of *A. buettneri* A.Berger, although more recent views (Carter 1994) consider the three as separate taxa. Milne-Redhead collected a further *Aloe* in 1938 that was subsequently described by Christian (1940a) as *A. milne-redheadii* Christian.

Reynolds visited Angola during June and July of 1959, but could not reach certain areas in the northeast and southeast of the country due to the inaccessibility of these areas. During his journey he established that *A. hereroensis* Engl., from Namibia and the Northern

Cape Province of South Africa, also occurs in Angola. An additional six species were described by Reynolds (1960, 1961, 1962, 1964) after his Angolan travels, all of which are still upheld.

During the early 1970s, Leach & Cannell collected *Aloe* material in Angola from which Leach (1971, 1974) described five new species and a new variety of *A. andongensis* Baker. At the same time Leach (1974) also described a further species of which the material was collected and given to him by Baptista de Sousa in 1973. All seven of these taxa are still considered current, although *A. esculenta* L.C.Leach is sometimes considered to be synonymous with *A. angolensis* (Glen & Hardy 2000).

IDENTIFICATION KEYS

Two identification keys are presented below. The first uses field characters for the identification of living plants, whereas the second uses mostly leaf and inflorescence characters (flowers, pedicels and floral bracts) and is aimed at identifying herbarium specimens. *Aloe venenosa* is not included in the identification keys owing to lack of information for this insufficiently known species.

Key using field characters

1a Acaulescent or with very short stem:

2a Leaf bases markedly enlarged below ground to form bulb-like swelling:

3a Leaves with marginal teeth ± 1 mm long, densely crowded; floral bracts ovate-acuminate *A. bulbicaulis*

3b Leaves with marginal teeth $\pm 3-4$ mm long, 5–40 mm apart; floral bracts linear-lanceolate *A. paedogona*

2b Leaf bases not markedly enlarged to form bulb-like swelling:

4a Flowers vertically disposed (secund) when open:

5a Inflorescence up to 1 m high; racemes subdense; flowers scarlet with a bloom, ± 40 mm long *A. guerrae*

5b Inflorescence 2.20–2.75 m high; racemes lax; flowers dull reddish purple, 28–33 mm long *A. procera*

4b Flowers horizontally or pendulously disposed when open:

6a Racemes capitate:

7a Leaves with copious small, white, circular spots near base on lower surface; leaf margin with small crowded teeth that are sometimes almost serrate *A. grata*

7b Leaves obscurely lineate, with few to many whitish spots scattered or arranged in transverse bands on lower surface; leaf margin with pungent, red-brown teeth *A. hereroensis* var. *hereroensis*

6b Racemes acuminate:

8a Leaves not marked with whitish spots on either surface:

9a Inflorescence ± 0.9 m long; flowers yellow, 20–25 mm long *A. angolensis*

9b Inflorescence longer than 1 m; flowers reddish pink, longer than 30 mm:

10a Flower buds at first covered by densely imbricate, long, white, prominently nerved bracts *A. metallica*

10b Flower buds not covered by dense floral bracts *A. christianii*

8b Leaves marked with whitish spots on one or both surfaces:

11a Leaves trifarious *A. dinteri*

11b Leaves not trifarious:

12a Leaves with prickles along median line of lower leaf surface *A. esculenta*

12b Leaves without prickles along median line of lower leaf surface:

13a Leaves copiously white-spotted on upper surface, usually obscurely spotted on lower surface; marginal teeth 4–7 mm long *A. zebrina*

13b Leaves densely white-spotted on both surfaces, especially on lower surface; marginal teeth 2–3 mm long ... *A. milne-redheadii*

1b Stems erect, procumbent, ascending or pendent:

14a Stems erect:

15a Leaves grass-like *A. nuttii*

15b Leaves not grass-like:

16a Stem usually shorter than 1 m:

17a Stem 0.5–1 m long; leaves obscurely lineate, rarely with few spots near base *A. scorpioides*

17b Stem up to 0.3 m long; leaves with spots arranged in wavy transverse bands *A. lepidia*

16b Stem usually longer than 1.5 m:

18a Stems without persistent dried leaves *A. rupicola*

18b Stems with persistent dried leaves:

19a Stem unbranched *A. littoralis*

19b Stem branched *A. palmiformis*

14b Stems procumbent, ascending or pendent:

20a Stems pendent:

21a Stems without persistent dried leaves; leaves obscurely lineate, without spots *A. mendesii*

21b Stems with persistent dried leaves; leaves obscurely lineate with few small, whitish, H-shaped spots; spots more numerous and in transverse bands on lower surface *A. inamara*

- 20b Stems procumbent, ascending:
- 22a Stems slender, branched, forming thickets:
- 23a Stems without persistent dried leaves *A. catengiana*
- 23b Stems with persistent dried leaves *A. gossweileri*
- 22b Stems branched, but not slender, not forming thickets:
- 24a Inflorescence 0.5–0.9 m high, unbranched or branched once, with lax racemes *A. vallis*
- 24b Inflorescence 0.3–0.4 m high, branched, with dense racemes:
- 25a Leaves sometimes sparsely spotted on lower surface, with many crowded spots near base, 200–250 × 60–70 mm, with marginal teeth 2–3 mm long, 5–7 mm apart; ovary pale green *A. andongensis* var. *andongensis*
- 25b Leaves more copiously white-spotted with spots tending to be arranged in wavy transverse bands, smaller and narrower than above, with marginal teeth smaller and more crowded; ovary brownish orange *A. andongensis* var. *repens*

Key using herbarium characters

- 1a Floral bracts longer than pedicels at anthesis:
- 2a Flowers 20–24 mm long; outer perianth segments free for < 10 mm; leaves 40–50 mm wide *A. angolensis*
- 2b Flowers longer than 25 mm; outer perianth segments free for > 10 mm; leaves wider than 60 mm:
- 3a Floral buds and open flowers secund:
- 4a Racemes ± 200 mm long; flowers ± 40 mm long, ± 8 mm across ovary; floral bracts 6–8 mm long; leaves 60–70 mm wide, with marginal teeth 4–5 mm long *A. guerrae*
- 4b Racemes 250–400 mm long; flowers 28–33 mm long, 5–6 mm across ovary; floral bracts 5–6 mm long; leaves 80–95 mm wide, with marginal teeth 1.5–3.5 mm long *A. procera*
- 3b Floral buds and open flowers not secund:
- 5a Leaves with blackish brown marginal teeth and similar spines along median line of lower leaf surface; pedicels 5–6 mm long; floral bracts 20–27 mm long *A. esculenta*
- 5b Leaves with reddish brown marginal teeth and no spines along median line of lower leaf surface; pedicels longer than 6 mm; floral bracts shorter than 20 mm:
- 6a Leaves up to 600 × 100–130 mm, with marginal teeth 3–4 mm long; inflorescence much-branched and rebranched; floral bracts 12–18 mm long *A. littoralis*
- 6b Leaves 250–400 × 70–90 mm, with marginal teeth 2–3 mm long; inflorescence sparsely branched; floral bracts 18–20 mm long *A. metallica*
- 1b Floral bracts shorter than or equal to pedicels at anthesis:
- 7a Floral bracts about as long as pedicels at anthesis:
- 8a Floral bracts almost equal to or slightly shorter than pedicels at anthesis; leaves < 50 mm wide:
- 9a Inflorescence up to 0.15 m long, simple or 1- or 2-branched, descending at base and then curving upwards; racemes rather dense; flowers 21–28 mm long, well constricted above ovary; outer perianth segments free for 8.5–10.0 mm *A. scorpioides*
- 9b Inflorescence 0.5–0.6 m long, simple or 1-branched, oblique or suberect; flowers 20–25 mm long, only slightly constricted above ovary; outer perianth segments free for 4.5–6.0 mm *A. vallis*
- 8b Floral bracts almost equal to pedicels at anthesis; leaves > 50 mm wide, usually > 60 mm wide:
- 10a Leaves 100–120 mm wide, unspotted; flowers 35–45 mm long, not constricted above ovary *A. christianii*
- 10b Leaves < 80 mm wide, spotted on both surfaces; flowers up to 35 mm long, abruptly constricted above ovary:
- 11a Leaf margin narrow, white, with minute white teeth, ± 0.5 mm long, 1–2 mm apart, edge of keel white cartilaginous with similar teeth *A. dinteri*
- 11b Leaf margin cartilaginous, with stout, pungent, red-brown teeth, 4–7 mm long, 10–15 mm apart, no spines on median line ... *A. zebrina*
- 7b Floral bracts markedly shorter than pedicels at anthesis:
- 12a Outer perianth segments free for ± ½ or > ½ its length:
- 13a Pedicel > 25 mm long at anthesis:
- 14a Flowers 25–33 mm long; outer perianth segments free for 14–16 mm *A. hereroensis* var. *hereroensis*
- 14b Flowers 35–42 mm long; outer perianth segments free almost to base, or for ¾ of its length *A. nuttii*
- 13b Pedicel < 20 mm long at anthesis:
- 15a Flowers ± 42 mm long *A. rupicola*
- 15b Flowers ± 25 mm long:
- 16a Pedicels 18–20 mm long; floral bracts ± 12 mm long *A. mendesii*
- 16b Pedicels 14–18 mm long; floral bracts 5–8 mm long:
- 17a Leaves 200–250 × 60–70 mm, with marginal teeth 2–3 mm long, 5–7 mm apart *A. andongensis* var. *andongensis*
- 17b Leaves smaller and narrower than above, with marginal teeth smaller and more crowded *A. andongensis* var. *repens*
- 12b Outer perianth segments free for < ½ its length:
- 18a Leaves with marginal teeth up to 1 mm long:
- 19a Flowers 35–40 mm long; pedicels ± 20 mm long; leaves ± 150 mm wide; acaulescent plant with leaf bases enlarging below ground to form bulb-like swelling *A. bulbicaulis*
- 19b Flowers 26–29 mm long; pedicels 22–27 mm long; leaves 40–50 mm wide; plants with branched stem, growing pendent on cliff faces *A. inamara*
- 18b Leaves with marginal teeth > 2 mm long:
- 20a Floral bracts 15–25 mm long; pedicels 25–30 mm long; acaulescent plants with leaf bases enlarging below ground to form bulb-like swelling *A. paedogona*
- 20b Floral bracts < 7 mm; pedicels usually < 20 mm; shrubs or if acaulescent, then leaf bases not enlarging below ground to form bulb-like swelling:
- 21a Floral bracts up to 3 mm long:
- 22a Leaves 70–80 mm wide; flowers 25–28 mm long *A. grata*
- 22b Leaves ± 50 mm wide; flowers ± 30 mm long:
- 23a Flowers subsecund when open; pedicels ± 10 mm long; leaves with marginal teeth spaced ± 15 mm apart *A. gossweileri*
- 23b Flowers nodding to pendulous, not subsecund when open; pedicels 13–15 mm long; leaves with marginal teeth spaced ± 10 mm apart *A. palmiformis*
- 21b Floral bracts 5 mm or longer:
- 24a Leaves ± 35 mm wide; racemes up to 160 mm long; pedicels ± 10 mm long *A. catengiana*
- 24b Leaves > 60 mm wide; racemes 200 mm or longer; pedicels longer than 13 mm:
- 25a Leaves with marginal teeth 3–7 mm long; flowers 25–29 mm long, ± 5.5 mm across ovary; outer perianth segments free for 5–6 mm *A. lepida*
- 25b Leaves with marginal teeth 2–3 mm long; flowers 28–35 mm long, ± 8 mm across ovary; outer perianth segments free for ± 10 mm *A. milne-redheadii*

TAXONOMY

^E**A. andongensis** Baker var. **andongensis** in Transactions of the Linnean Society of London 1: 263 (1878). Type: Angola, Pungo Andongo, *Welwitsch* 3729 (BM, holo.!; K!, LISC!, LISU!, iso.).

Branched shrub. *Stem* short or 0.3–0.6 m high, branched, ascending, sometimes becoming decumbent, with persistent dried leaves. *Leaves* rosulate at branch apices, varying from spreading and slightly recurved to suberectly spreading and compact, dull grey-green, upper surface mostly without spots, sometimes sparsely spotted, lower surface usually with many crowded spots near base, lanceolate-attenuate, 200–250 × 60–70 mm; margin slightly cartilaginous, with brownish teeth 2–3 mm long, 5–7 mm apart; leaf exudate crusty when dry. *Inflorescence* 0.3–0.4 m high, erect, 2- or 3-branched. *Raceme* subcapitate to cylindrical-acuminate, 60–120 mm long, dense. *Floral bracts* 5–8 × 3 mm. *Pedicels* 14–18 mm long. *Flowers*: perianth pale orange-scarlet, paler at tips, 25 mm long, 5–6 mm across ovary, narrowed above ovary, widening towards mouth giving a clavate appearance, cylindric and very slightly decurved; outer segments free for 17 mm. *Stamens* exerted up to 1 mm. *Style* exerted up to 1–2 mm. *Flowering time*: January to April.

Diagnostic characters: upper leaf surface mostly without spots, sometimes sparsely spotted, lower surface usually with many crowded spots near the base. Buds all spread somewhat horizontally or slightly deflexed. Inflorescence subdense, subcapitate, with flowers lacking a basal swelling.

Relationships with other species: Reynolds (1966) placed *Aloe andongensis* in his Group 19: Plants of shrubby growth. It seems to be closely related to *A. lepida* L.C.Leach and also shows a strong link in vegetative characters with *A. squarrosa* Baker from Socotra (Leach 1974).

Habitat: exposed rocky places.

Distribution: endemic to Angola (Cuanza Sul, Huambo, Malange) (Figure 2).

Illustrations: Reynolds: 347 (1966).

Additional specimens examined

ANGOLA.—0915: Pungo Andongo, (–DA), 22 March 1973, *Bamps, Martins & Silva* 4246 (LISC, PRE), 31 March 1967, *Barbosa* 11332 (LISC), 29 December 1911, *Gossweiler* 5445 (LISC), 14 May 1960, *Reynolds* 9385 (BM, PRE). 1014: Cuanza Sul, Gabela, rocha Chitandero, na Roça Africana de CADA, (–CD), 16 March 1967, *Teixeira* 11203 (LISC). 1015: Benguela Province, 14 miles [22.5 km] S of Quibala, (–CC), 18 June 1960, *Reynolds* 9366 (BM). 1115: Cuanza Sul, 4 miles [6.5 km] NW of Cassongue, (–CC), 26 May 1960, *Reynolds* 9335 (BM, PRE). 1215: Huambo, Alto Hama, Iumbo, Rio Queve, (–BA), 6 April 1966, *Correia* 3638 (LISC).

^E**A. andongensis** Baker var. **repens** L.C.Leach in Journal of South African Botany 40: 115 (1974). Type: Angola, Cuanza Sul, 11 km E of Gabela, 8 June 1973, *Leach & Cannell* 13950 (LISC, holo.!; BM!, BR!, K!, PRE!, SRGH, iso.).

Branched shrub, forming large spreading clumps. *Stem* up to 0.6 m high, branched freely from base and above, prostrate, with persistent dried leaves. *Leaves* rosulate at branch apices, widely spreading, dull grey-green, upper surface mostly without spots, sometimes sparsely spotted, lower surface usually with copious

crowded spots near base, spots tend to be arranged in wavy transverse bands, lanceolate-attenuate, smaller and narrower than typical variety; margin slightly cartilaginous, with brownish teeth smaller and more crowded than typical variety; exudate crusty when dry. *Inflorescence* 0.3–0.4 m high, erect, 2- or 3-branched. *Raceme* subcapitate to cylindrical-acuminate, 60–120 mm long, dense. *Floral bracts* 5–8 × 3 mm. *Pedicels* 14–18 mm long. *Flowers*: perianth pale orange-scarlet, paler at tips, 25 mm long, 5–6 mm across ovary, narrowed above ovary, widening towards mouth giving a clavate appearance, cylindric and very slightly decurved; outer segments free for 17 mm. *Stamens* exerted up to 1 mm. *Style* exerted up to 1–2 mm. *Flowering time*: February to April.

Diagnostic characters: prostrate habit. Stems up to 0.6 m long, branching freely from the base and above, thus forming large spreading clumps. Stems foliate for greatest part of their length. Leaves much smaller, narrower, and more widely spreading than typical variety of species, also more copiously white-spotted with spots tending to be arranged in wavy transverse bands, with smaller, more crowded marginal teeth. Buds all spread somewhat horizontally or slightly deflexed. Inflorescence subdense, subcapitate, with flowers lacking a basal swelling. Ovary brownish orange.

Relationships with other species: see comments under *Aloe andongensis* subsp. *andongensis*.

Habitat: slopes of rounded granite hills.

Distribution: endemic to Angola (Cuanza Sul) (Figure 3).

Illustrations: Leach: 116 (1974).

Additional specimens examined

ANGOLA.—1114: Cuanza Sul, Santa Comba-Amboiva, bac du Queve, (–DB), 28 March 1973, *Bamps & Martins* 4301 (LISC). 1115: Cuanza Sul, Santa Comba, próximo de Santa Comba, (–AC), 10 March 1965, *Santos* 1412 (LISC).

^E**A. angolensis** Baker in Transactions of the Linnean Society of London 1: 263 (1878). Type: Angola, Barra do Bengo, between Quisoma and Cacucaco at Mutolo in District Quicuxe, 1858, *Welwitsch* 3728 (BM, holo.!; G!, K!, LISC!, LISU!, iso.).

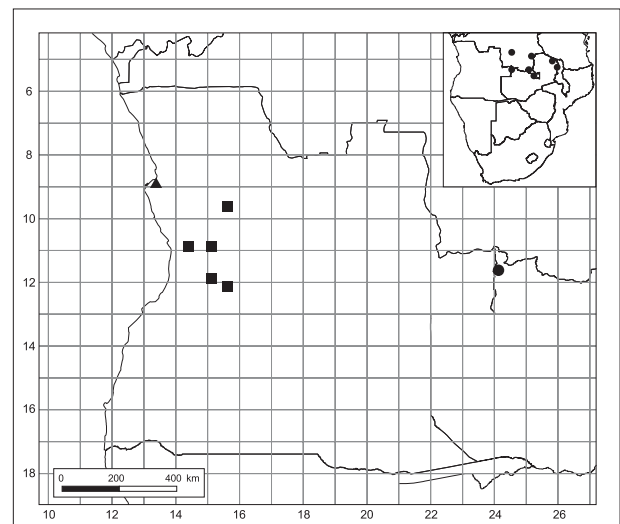


FIGURE 2.—Distribution of *Aloe andongensis* var. *andongensis*, ■; *A. angolensis*, ▲; and *A. bulbicaulis*, ●.

Stem very short or up to 0.7 m high. *Leaves* densely rosulate, suberect, glaucous, not spotted below, very fleshy, lanceolate-ensiform, 600 × 40–50 mm; margin with teeth, 2 mm long, 15–20 mm apart. *Inflorescence* 0.9 m high, erect, simple or up to 3-branched. *Raceme* cylindrical, slightly acuminate, 100 mm long, dense. *Floral bracts* 10 mm long. *Pedicels* 3–6 mm long. *Flowers*: perianth sulphur-yellow, 20–24 mm long; outer segments fused to beyond middle (free for less than 10 mm). *Stamens* and *style* scarcely exerted. *Flowering time*: unknown.

Diagnostic characters: thick leaves and branched inflorescence with dense racemes of sulphur-yellow flowers.

Relationships with other species: Reynolds (1966) stated that the affinities of this species are uncertain, but noted that the thick leaves and type of inflorescence suggest a link with the *Aloe littoralis*-complex. Reynolds (unpublished notes at PRE) further speculated that *A. angolensis* might be a natural hybrid between *A. littoralis* and *A. zebrina* Baker. This view is upheld by Glen & Hardy (2000), although they regarded it as conspecific with *A. esculenta* L.C. Leach. Carter (2001) considered it as a synonym of *A. littoralis*.

Habitat: low hills facing the Bengo River valley, not far from the sea.

Distribution: endemic to Angola (Bengo) (Figure 2).

Notes: this species has not been found again since Welwitsch collected the type specimen. A specimen collected on steep limestone slopes facing the sea between the Dande River Mouth and the road to Caxito, north of Luanda [Barbosa & Santos 10833 (LISC)] is considered to possibly be *Aloe angolensis*. However, this specimen was not in flower and had dry, dehiscent capsules. Until such time as flowering plants are found at this locality, it is not possible to say if this specimen belongs to *A. angolensis* or not (Reynolds 1966; Reynolds, unpublished notes at LISC).

A. bulbicaulis Christian in The Flowering Plants of South Africa 16: t. 630 (1936). Type: Zambia, West-

ern Province, Misundu Siding, *Porter cult. Christian PRE20587* (PRE, holo.!).

A. buettneri auct., sensu Reynolds (1966), p.p. ref. loc. in DRC, Malawi & Zambia.

Acaulescent, up to 0.5 m high, with leaf bases enlarged below ground to form bulb-like swelling; rosettes solitary. *Leaves* rosulate, deciduous, spreading, bright green, longitudinally striate, slightly fleshy, surface smooth, ovate-lanceolate, up to 500 mm long, 150 mm wide at middle; margin white, cartilaginous, with densely crowded, fairly evenly-spaced, whitish teeth, 1 mm long, 1–5 mm apart. *Inflorescence* up to 0.6 m high, erect, 3- or 4-branched. *Raceme* cylindrical, 100–200 mm long, lax below, more dense above. *Floral bracts* 8–15 × 5–8 mm. *Pedicels* ± 20 mm long. *Flowers*: perianth pale yellow to pinkish or brownish yellow with darker nerves, 35–40 mm long, 8–10 mm across ovary, slightly constricted above ovary, widening towards wide-open mouth, cylindrical; outer segments free for one-third (12–13 mm). *Stamens* scarcely exerted. *Style* slightly exerted. *Flowering time*: February.

Diagnostic characters: underground bulb. Leaves up to 500 mm long, 150 mm wide in middle, with densely crowded teeth of 1 mm long. Floral bracts ovate-acuminate, 8–15 mm long.

Relationships with other species: Reynolds (1966) considered *Aloe bulbicaulis* to be conspecific with *A. buettneri* together with *A. paedogona*. Carter (1994) stated that the three taxa are morphologically clearly distinct and also separated geographically and therefore does not agree with Reynold's opinion that the three taxa are conspecific.

Habitat: seasonally wet grassland in open woodland.

Distribution: Eastern Angola (Moxico), southeastern Democratic Republic of the Congo (Katanga), northern Malawi, northwestern Mozambique, southwestern Tanzania, northern Zambia (Figure 2).

Illustration: Lane: 17 (2004).

Notes: cited in Carter (1994) to occur in western Angola. This is clearly a mistake and should be eastern Angola. It has been collected in western Zambia, at Matonchi Farm [Milne-Redhead 2903A (K–PRE, photo.); Christian 868 (PRE)] very close to the Angolan border.

A. catengiana Reynolds in Kirkia 1: 160 (1961). Type: Angola, Benguela District, at Catengue, 60 miles [96 km] SE of Benguela, 2 August 1960, Reynolds 9307 (PRE, holo.!, K, iso.!).

Shrub, forming dense, tangled thickets of 1–2 m across. *Stem* 1.5–2.0 m long, simple or branching low down, slender, ascending, divergent or sprawling, dried leaves not persistent. *Leaves* rather laxly rosulate on apical 0.3 m of stem, spreading to deflexed near base, pale yellowish grey-green, with copious, very pale green lenticular spots on both surfaces, more numerous towards base, narrowly lanceolate-attenuate, ± 300 × ± 35 mm; sheath lineate, 15–20 mm long; margin with firm, pale, reddish brown-tipped teeth, 3 mm long, 8–10 mm apart. *Inflorescence* 0.4 m high, erect or suberect, slender, divaricately about 6-branched. *Raceme* cylindrical-acuminate, terminal raceme longest, 160 mm long, erect, lateral racemes shorter, oblique, rather lax, flowers sub-

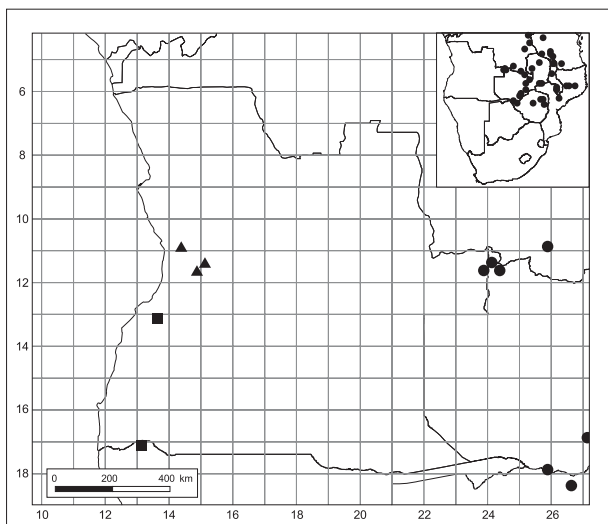


FIGURE 3.— Distribution of *Aloe andongensis* var. *repens*, ▲; *A. catengiana*, ■; and *A. christiani*, ●.

secund on lateral racemes. *Floral bracts* 5 × 3 mm. *Pedicels* 10 mm long. *Flowers*: perianth dull scarlet, 28 mm long, 7 mm across ovary, slightly narrowed above ovary, slightly enlarging towards mouth, cylindric, slightly decurved; outer segments free for 10 mm. *Stamens* exerted 1–2 mm. *Style* exerted up to 2 mm. *Flowering time*: March to July.

Diagnostic characters: forms dense, tangled thickets. Stems slender. Leaves peculiar pale yellowish grey-green, usually copiously spotted on both surfaces. Inflorescence slender and divaricately branched. Racemes vary from terminal erect with flowers evenly distributed around axis, to oblique with flowers somewhat secund.

Relationships with other species: its closest ally is *Aloe palmiformis* (Reynolds 1961).

Habitat: hot, arid bush country and quartzitic sandstone cliffs.

Distribution: western Angola (Benguela, Namibe), northern Namibia (Figure 3).

Illustration: Reynolds: 373 (1966).

Notes: this species was previously only known from the type locality and considered to be endemic to Angola. However, it has recently been discovered in the Kaokoveld in Northern Namibia [E. van Jaarsveld 18805 (WIND)].

A. christianii Reynolds in Journal of South African Botany 2: 171 (1936a). Type: Zimbabwe, Ewanrigg, E of Harare, Acturus, May–June 1936, Reynolds 1885 (PRE, holo.!, K!, SAM!, SRGH, iso.).

Acaulescent; rosettes usually solitary, up to 1 m across, or in small groups, rarely suckering. *Stem* develops in older plants, up to 1 m long, erect or decumbent, with persistent dried leaf bases. *Leaves* densely rosulate, erectly spreading, dull green above, dull bluish green below, tinged pinkish in dry conditions, unspotted but often obscurely lineate, lanceolate-attenuate, 300–600 mm long, 100–120 mm wide at base; margin cartilaginous, with pungent, pinkish to pale brown, brown-tipped teeth, 2–5 mm long, 10–20 mm apart. *Inflorescence* 2–3 m high, erect, compactly 6–10-branched, lower branches sometimes 1- or 2-rebranched. *Raceme* cylindric-acuminate, 150–300 mm long, terminal raceme longest, lateral racemes shorter, dense. *Floral bracts* 8–18 × 3–4 mm. *Pedicels* 8–20 mm long. *Flowers*: perianth bright coral-pink with a bloom and obscure nerves, lighter and brownish at tips, 35–45 mm long, 8–10 mm across ovary, not narrowed above ovary, cylindric-trigonus, straight; outer segments free for 15 mm. *Stamens* exerted 3–4 mm. *Style* exerted 4–5 mm. *Flowering time*: April to July.

Diagnostic characters: rosette large. Inflorescence tall and branched. Floral bracts small, up to 18 mm long, pedicels short, 8–20 mm long. Flowers cylindric-trigonus, with thick, fleshy perianth and outer segments free for only 15 mm.

Relationships with other species: *Aloe christianii* is closely related to *A. pretoriensis* Pole Evans from northern South Africa and Zimbabwe (Reynolds 1966).

Habitat: usually in shade in woodland, sometimes in tall grassland, never on rocks.

Distribution: eastern Angola (Moxico), southern and eastern Democratic Republic of the Congo, Malawi,

northern Mozambique, eastern Tanzania, Zambia, northern Zimbabwe (Figure 3).

Illustrations: Reynolds: 187, 188 (1966); Lane: 32 (2004).

Notes: this species has not yet been collected in Angola, but it was reportedly seen in Angola near the Zambian border west of Matonchi by Mr Edgar Milne-Redhead (Reynolds 1966; Carter 2001).

A. dinteri A. Berger in Dinter, Neue und wenig bekannte Pflanzen Deutsch-Südwest-Afrikas: 14 (1814). Type: Namibia, Outjo, Dinter 2791a (SAM, holo.).

Acaulescent, 0.26 m high; rosettes solitary. *Leaves* trifarious, spreading to almost horizontal, chocolate-brown or deep brownish green, copiously spotted with crowded narrowly elongated white spots arranged ± in broken transverse bands, with small white teeth on white cartilaginous edge of keel, narrowly lanceolate-acuminate, plicate-carinate, 200–300 mm long, 50–80 mm wide at base; margin narrow, white, with minute white teeth, ± 0.5 mm long, 1–2 mm apart. *Inflorescence* 0.5–0.85 m high, erect, 3–8-branched. *Raceme* cylindric-acuminate, 150–200 mm long, terminal raceme the longest, lax. *Floral bracts* 7–12 × ± 2 mm. *Pedicels* 10–15 mm long. *Flowers*: perianth pale rose-pink with bluish bloom, pale to almost white at mouth, 28–30 mm long, ± 6.5 mm across ovary, abruptly narrowed above ovary, enlarging towards mouth, slightly decurved; outer segments free for 5–10 mm. *Stamens* included or exerted up to 1 mm. *Style* exerted up to 1 mm. *Flowering time*: January to March.

Diagnostic characters: acutely folded, trifarious, chocolate-brown leaves of up to 300 mm long, with margins finely toothed. Inflorescence 3–8-branched and up to 0.85 m high. Floral bracts 3-nerved.

Relationships with other species: *Aloe dinteri*, together with its close relatives, *A. sladeniana* Pole Evans from central Namibia and *A. variegata* L. from southern, western and central South Africa and southern Namibia, forms the Section *Serrulatae* Salm-Dyck (Glen & Hardy 2000).

Habitat: usually wedged firmly in cracks in limestone in areas of very low summer rainfall. Sometimes on granite, in bushveld near edge of Namib Desert.

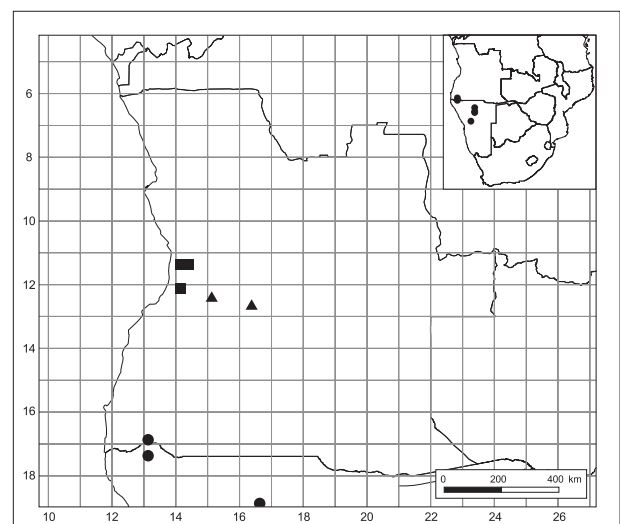


FIGURE 4.— Distribution of *Aloe dinteri*, ●; *A. gossweileri*, ■; and *A. grata*, ▲.

Distribution: southwestern Angola (Namibe, Cunene), northern Namibia (Figure 4).

Illustrations: Reynolds: t. 637 (1936b); Reynolds: 211 (1950); Rothmann: 58, 59 (2004).

Note: this species was previously considered to be endemic to northern Namibia and occurs near the Cunene River west of Ruacanã. Due to its frequent proximity to the river, it was believed likely to occur north of the Cunene River in Angola (Hardy 1992). In fact, a few plants were reportedly seen near Namibe (Moçâmedes) on low stony ridges and in stony desert areas (Downs 1970). However, no herbarium specimens could be found to confirm this distribution. Clair Bell (pers. comm.) saw this species north of the Cunene River in Angola in 1996. A plant collected during this expedition is currently growing in the Botanical Society Conservatory at Kirstenbosch National Botanical Gardens, Cape Town (SW Angola, July 1996, *Clair Bell 1120/96*). However, opinions are divided on the correct identification of this taxon in Angola. According to John Lavranos (pers. comm.) a plant collected inland from Namibe by Dr Philip Downs in 1971 suckered freely and did not have the solitary rosettes characteristic of *Aloe dinteri*. Furthermore, it bore leaves of no longer than 50–70 mm and consistently produced simple inflorescences. Lavranos, therefore, considers it to be closer to *A. sladeniana*.

A. esculenta L.C. Leach in Journal of South African Botany 37: 249 (1971). Type: Angola, near Pereira d'Eça, 7 August 1967, *Leach & Cannell 13818* (PRE, holo.!, BM, K!, LISC!, SRGH, iso.).

Acaulescent or sometimes with short, thick, often decumbent stem, up to 0.4 m long; rosettes suckering to form dense clumps. *Leaves* condensed rosulate, erectly spreading or recurved, greyish green, with pinkish brown tinge in dry conditions, densely white-spotted on both surfaces, spots more copious on lower surface, arranged in irregular transverse bands, pungent blackish brown spines along median line, lanceolate, up to 500 mm long, 80 mm wide at base; margin with pungent, blackish brown teeth, 3–5 mm long, 10–20 mm apart; leaf exudate not bitter. *Inflorescence* up to 2 m high, erect, 3–5-branched, lower branches sometimes sparsely rebranched. *Raceme* cylindrical-acuminate, 300–500 mm long, lax. *Floral bracts* 20–27 × 10–11 mm. *Pedicels* 5–6 mm long. *Flowers*: perianth pink with cream-coloured stripes, becoming yellowish when mature, 28–30 mm long, ± 6 mm across ovary, enlarging towards middle, distinctly subclavate; outer segments free for 15–18 mm. *Stamens* exerted up to 6 mm. *Style* exerted up to 8 mm. *Flowering time*: July to August.

Diagnostic characters: spotted aloe. Acaulescent plants forming clumps, frequently of shrubby habit. *Leaves* copiously white-spotted, with large spots arranged in transverse bands. Strong blackish brown spines along median line on underside of leaf. *Flowers* distinctly subclavate; stigma exerted up to 8 mm.

Relationships with other species: at first sight this species looks very much like a stemless form of *Aloe littoralis*, to which it is closely allied. Leach (1971) stated that it may well be considered as an ecologically separated subspecies of *A. littoralis*. Glen & Hardy (2000) regarded it as conspecific with *A. angolensis*, with the latter name

taking priority according to the rules of the International Code of Botanical Nomenclature (McNeill 2006).

Habitat: sandy soils of flats of inland drainage areas.

Distribution: southern Angola (Cunene, Huila), north-western Botswana, northern Namibia, southwestern Zambia (Figure 5).

Illustrations: Rothmann: 62, 63 (2004).

Additional specimens examined

ANGOLA.—1515: Huila, (–AC), *Carriso & Sousa 193* (LISC). 1614: Huila, Roçadas, (–DB), 8 July 1970, *Menezes 3384* (K, LISC, PRE, SRGH); Cunene, Cuamato, Roçadas, entre Dimba e Humbe, (–DB), 20 July 1970, *Santos & Barroso 2761* (LISC, PRE). 1715: Baixo Cunene, Cuamato, Roçadas, a 34 km para a Missão do Cuamato, (–AA), 1 July 1970, *Santos & Barroso 2695* (LISC, PRE); Huila, Roçadas, Cuamato, (–AA), 4 July 1970, *Menezes 3379* (LISC, PRE); Baixo Cunene, Cuanhama, Pereira d'Eça, entre Namacunde e Chiede, (–BB), 9 July 1970, *Santos & Barroso 2717* (LISC, PRE).

^EA. gosseweileri Reynolds in Journal of South African Botany 28: 205 (1962). Type: Angola, Cuanza Sul District, Seles, 7 miles [11 km] SE of Vila Nova de Seles, 15 July 1961, *Reynolds 9760* (PRE, holo.!, K!; LISC!, iso.).

Thicket-forming shrub. *Stem* 1.0–1.5 m long, branching from ground level only, ascending or divergent, without persistent dried leaves. *Leaves* subdensely rosulate at branch apices, spreading to slightly recurved, green, mostly without spots, lanceolate-attenuate, ± 300 mm long, 50 mm wide at base; margin with pale deltoid teeth, 3–4 mm long, 15 mm apart. *Inflorescence* 0.4–0.5 m high, erect, pyramidal, divaricately 6–8-branched. *Raceme* cylindric-acuminate, 100–150 mm long, terminal raceme the longest, dense, flowers subsecund when open. *Floral bracts* 3 × 2 mm. *Pedicels* 10 mm long. *Flowers*: perianth scarlet, paler at tips, 30 mm long, 6 mm across ovary, very slightly narrowed above ovary, slightly enlarging towards trigonal mouth; outer segments free for 10–12 mm. *Stamens* exerted 1–2 mm. *Style* exerted 2–3 mm. *Flowering time*: March.

Diagnostic characters: forms thickets. Stems branched at ground level only, 1.0–1.5 m long. *Inflorescence* divaricately branched, pyramidal with almost horizontal racemes with subsecund flowers.

Relationships with other species: its closest ally appears to be *Aloe palmiformis* (Reynolds 1966).

Habitat: rocky hills.

Distribution: endemic to Angola (Benguela, Cuanza Sul) (Figure 4).

Illustrations: Reynolds: 372 (1966).

Additional specimens examined

ANGOLA.—1114: Vila Nova de Seles, (–AD), March 1941, *Gosseweiler 13313* (LISC, para.). 1214: Benguela, Bocoio, a caminho da povoação da Chicuma, andados ± 40 km da povoação de Chila, (–AA), 24 May 1973, *Raimundo, Matos & Figueira 1415* (LISC).

^EA. grata Reynolds in Journal of South African Botany 26: 87 (1960). Type: Angola, Bié District, 30 miles [48 km] S of Chinguar, on Chimbandu Hill, 19 June 1959, *Reynolds 9246* (PRE, holo.!, K!; LUA, iso.).

Acaulescent or with short stem, suckering to form dense groups of rather compact rosettes. *Leaves* densely rosulate, erect to erectly spreading, upper surface green,

tinged reddish brown, without spots, lower surface paler glaucous green, with many crowded, pale green, circular, 1 mm spots in lower quarter, lanceolate-attenuate, 200–250 × 70–80 mm; margin sinuate-dentate, sometimes almost serrate, with teeth 2–3 mm long, 5–8 mm apart; leaf exudate drying pale yellow. *Inflorescence* 0.7–0.9 m high, erect, simple in young plants, up to 3-branched in older plants. *Raceme* capitate or subcapitate, 80–100 mm long, fairly dense. *Floral bracts* 2 × 1.5 mm. *Pedicels* ± 20 mm long. *Flowers*: perianth scarlet, 25–28 mm long, 6 mm across ovary, slightly narrowed above ovary, enlarging towards middle, slightly narrowing at mouth, trigonous; outer segments free for 7 mm. *Stamens* exerted 1–2 mm. *Style* exerted 2–3 mm. *Flowering time*: June.

Diagnostic characters: leaves with small crowded marginal teeth that are sometimes almost serrate, lower surface with copious white, small, circular spots near base. Inflorescence simple in young plants, forked in older plants, 2- or 3-branched in largest specimens. Racemes capitate or almost so. Perianth scarcely trigonously indented above ovary. Floral bracts 2 mm long, 1-nerved.

Relationships with other species: the nearest ally to this species seems to be *Aloe mzimbana* Christian from central and southeastern tropical Africa (Reynolds 1966).

Habitat: hillsides, mostly on rocks.

Distribution: endemic to Angola (Benguela, Bié, Huambo) (Figure 4).

Illustration: Reynolds: 117 (1950).

Additional specimen examined

ANGOLA.—1215: Benguela, Serra do Moco, (–AC), 3 June 1940, Gossweiler 12597 (LISC).

A. guerrae Reynolds in Journal of South African Botany 26: 85 (1960). Type: Angola, Bié District, E of General Machado, 18 June 1959, Reynolds 9218 (PRE, holo.!; K!, LUAI, iso.).

Acaulescent or with very short stem; rosettes single, usually slightly tilted to one side. Leaves densely rosulate, suberectly spreading to spreading with slightly recurved apical portion, dull green, obscurely lineate on upper surface, grey-green with no markings on lower surface, lanceolate-attenuate, ± 400 mm long, 60–70 mm wide at base; margin with pungent, pale brown or reddish brown teeth, 4–5 mm long, 10–15 mm apart; leaf exudate drying yellow. *Inflorescence* 0.9–1 m high, erect, divaricately 8–10-branched, lower branches sometimes rebranched. *Raceme* cylindrical, ± 200 mm long, oblique to almost horizontal, dense, buds and flowers secund, almost erect. *Floral bracts* 6–8 × 4 mm. *Pedicels* ± 5 mm long. *Flowers*: perianth scarlet with a bloom, 40 mm long, 8 mm across ovary, scarcely narrowed above ovary, cylindric-trigonous towards slightly upturned mouth, straight or slightly curved; outer segments free for 10–12 mm. *Stamens* exerted up to 2 mm. *Style* exerted up to 3 mm. *Flowering time*: May to June.

Diagnostic characters: inflorescence divaricately branched with oblique to subhorizontal racemes of secund flowers.

Relationships with other species: its nearest ally is *Aloe secundiflora* Engl. from eastern and northeastern Africa (Reynolds 1966).

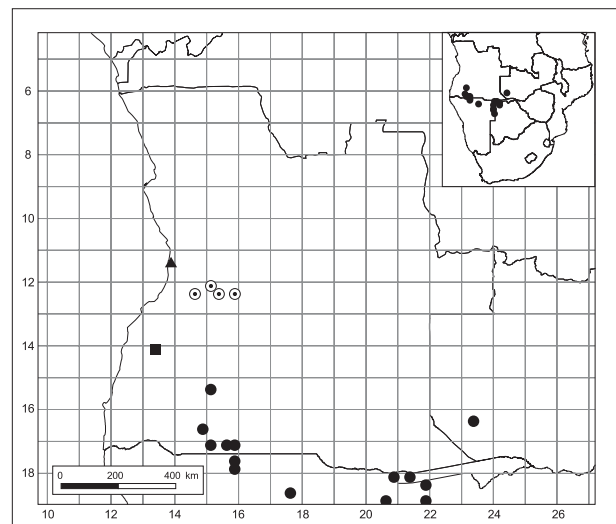


FIGURE 5.—Distribution of *Aloe esculenta*, ●; *A. guerrae*, ○; *A. inamara*, ▲; and *A. vallis*, ■.

Habitat: grassland with scattered bushes.

Distribution: endemic to Angola (Benguela, Huambo) (Figure 5).

Illustration: Reynolds: 229 (1966).

Additional specimens examined

ANGOLA.—1214: Balombo, 23 miles [37 km] E of Monte Belo, 6 miles [9.6 km] W of Balombo, (–BC), 3 July 1959, Reynolds 9325 (PRE). 1215: Benguela, Nova Lisboa, (–AA), 9 May 1937, Exell & Mendonça 1677 (LISC); Benguela, Calupiano, (–AD), 31 May 1940, Gossweiler 12600 (LISC); Bié Province, Posto do Cunje, near Silva Porto, (–BD), 1 August 1955, Reynolds 6885 (PRE).

A. hereroensis Engl. in Botanische Jahrbücher 10: 2 (1888), var. **hereroensis**. Type: Namibia, Usakos, 28 May 1886, Marloth 1438 (B, holo.!; NBG!, PRE!, iso.).

Acaulescent; rosettes solitary or suckering to form small clumps. Stem sometimes develops in older plants, up to 1 m long, simple or branched, procumbent, with persistent dried leaves. Leaves densely rosulate, arcuate erect, greyish green or often bronzed, obscurely lineate, usually without spots on upper surface, few to many irregularly scattered single or double H-shaped whitish spots on lower surface, ovate-lanceolate, 300–400 mm long, 60–90 mm wide at base; margin slightly cartilaginous, with pungent, reddish brown, spreading, sometimes bifid teeth, 3–4 mm long, 8–12 mm apart. *Inflorescences* up to 1 m high, erect, 4–8-branched, lower branches rebranched. *Raceme* corymbose-capitate, 60–80 mm long, very dense. *Floral bracts* 20–25 × 3–4 mm. *Pedicels* 30–50 mm long. *Flowers*: perianth scarlet, sometimes orange, 25–35 mm long, 8–9 mm across ovary, widening slightly towards middle, narrowing slightly towards upturned mouth, cylindric-trigonous; outer segments free for 14–16 mm. *Stamens* exerted 2–4 mm. *Style* exerted up to 5 mm. *Flowering time*: June to September.

Diagnostic characters: leaves obscurely lineate with spotted lower surface. Much branched inflorescence with short, broad racemes. Flowers distinctly shaped, with upturned mouth, red or sometimes orange.

Relationships with other species: *Aloe hereroensis* is included in Section *Asperifoliae* (A. Berger) Glen &

D.S.Hardy and is closely allied to *A. viridiflora* Giess from central Namibia (Glen & Hardy 2000).

Habitat: arid, stony desert conditions with very low rainfall. Usually grows on quartzite, but has been found on dolomite in the Kalahari. Confined to summer rainfall area.

Distribution: southwestern Angola (Huambo, Namibe), Namibia, South Africa (Northern Cape, Free State) (Figure 6).

Illustrations: Reynolds: 101 (1966); Rothmann: 66, 67 (2004).

Additional specimens examined

ANGOLA.—1215: Huambo, entre Alto Hama e Águas Quentes, (–BA), 20 August 1967, *Silva 2104* (LISC). 1512: Moçâmedes, andados 30 km de Moçâmedes para Dois Irmãos, (–AB), 2 May 1960, *Mendes 3898* (LISC); Benguela Province, 20 miles [32 km] NE of Moçâmedes, (–AB), 28 June 1959, *Reynolds 9283* (PRE); Moçâmedes, Caraculo, a $\pm$ 25 km para Moçâmedes, (–AB), 7 May 1962, *Santos 1007* (LISC, SRGH); Moçâmedes, Reserva de Moçâmedes junto ao limite NE, (–DA), 5 March 1969, *Teixeira 12871* (LISC); Moçâmedes, Reserva de Moçâmedes, (–DA), 11 April 1969, *Teixeira 12942* (LISC).

^E**A. inamara** L.C.Leach in Journal of South African Botany 37: 259 (1971). Type: Angola, Cuanza Sul District, S of Novo Redondo, at mouth of Quicombo River, 11 October 1970, *Leach & Cannell 14608* (LISC, holo.!, PRE, iso!).

Plants hanging on cliff faces. *Stem* up to 2 m long, pendent, branching at base and more sparsely above, forming dense mats, without persistent dried leaves. *Leaves* rosulate on branch apices, widely spreading, curved with apices pointing downwards, pale yellowish green, turning brown when exposed, obscurely lineate with few small, whitish, H-shaped spots, more spots in transverse bands on lower surface, falcate, 450–600 $\times$ 40–50 mm; margin whitish or faint pink, with whitish, often brown-tipped teeth, 0.3–1 mm long, 4–20 mm apart; leaf exudate yellow, not bitter. *Inflorescence* 0.4–0.55 m long, pendulous with tip upturned, 4–6-branched. *Raceme* shortly cylindrical-conical to almost subcapitate, terminal raceme $\pm$ 75 mm long, lateral racemes shorter, arcuate-ascending, lax. *Floral bracts* 7.5–9.0 $\times$ $\pm$ 3 mm. *Pedicels* 22–27 mm long. *Flowers*: perianth dull red with greenish tips, becoming somewhat yellowish with age, 26–29 mm long, 8 mm across ovary, abruptly narrowed above ovary, enlarging towards middle, narrowing again at mouth, slightly decurved, basally truncate and inflated; outer segments free for 6.5–8.0 mm. *Stamens* not or only rarely slightly exerted. *Style* scarcely or not exerted. *Flowering time*: apparently an extended period including October.

Diagnostic characters: leaves obscurely lineate with H-shaped spots. Racemes short, sometimes almost subcapitate. Pedicels 22–27 mm long. Flowers dull red with much inflated truncate base and genitalia scarcely or not exerted.

Relationships with other species: its nearest ally appears to be *Aloe swynnertonii* Rendle from eastern south tropical Africa (Leach 1971).

Habitat: almost vertical cliff faces.

Distribution: endemic to Angola (Cuanza Sul) (Figure 5).

Illustrations: Leach: 261, 263, 264 (1971).

Notes: this species is only known from the type locality.

^E**A. lepida** L.C.Leach in Journal of South African Botany 40: 102 (1974). Type: Angola, Huambo District, Morro de Sume, $\pm$ 27 km SSE of Nova Lisboa, 15 February 1973, *Baptista de Sousa s.n. in Leach 14538A* (LISC, holo.!, SRGH, iso.).

Low, much-branched shrub, up to 0.3 m high. *Stem* branching at base, stout, erect, without persistent dried leaves. *Leaves* densely rosulate at branch apices, widely spreading, rigidly strongly recurved, bright to dark yellowish deep green, conspicuous but irregular white spots in wavy transverse bands, spots smaller and more numerous on lower surface, broadly ovate-attenuate, 200–280 $\times$ 75–90 mm; margin with pungent, brown-tipped teeth with whitish base, 3–7 mm long, 6–12 mm apart; exudate crusty when dry. *Inflorescence* 0.3–0.5 m high, erect, 1- or 2-branched. *Raceme* cylindrical-acuminate, $\pm$ 200 mm long, lax. *Floral bracts* 6–7 $\times$ 3.0–3.5 mm. *Pedicels* 15–20 mm long. *Flowers*: perianth pale orange-scarlet, somewhat yellowish striped, 25–29 mm long, $\pm$ 5.5 mm across ovary, narrowed above ovary, enlarging towards wide open mouth, cylindric, slightly curved; outer segments free for 5–6 mm. *Stamens* not exerted. *Style* only occasionally very shortly exerted. *Flowering time*: February to May.

Diagnostic characters: leaves dark yellowish green, strongly recurved, conspicuously marked with irregular transverse wavy bands of whitish spots, armed with large marginal teeth. Inflorescence with lax, cylindric-acuminate racemes, with buds quickly nodding. Flower slender with outer segments free for 5–6 mm, with mouth widely open, stamens included and stigma only occasionally very shortly exerted.

Relationships with other species: *Aloe lepida* seems to be closely related to *A. andongensis* and also shows a strong link in vegetative characters with *A. squarrosa* Baker from Socotra (Leach 1974).

Habitat: rocky slopes in shade of trees.

Distribution: endemic to Angola (Huambo) (Figure 6).

Illustrations: Leach: 103, 104, 105 (1974).

Additional specimen examined

ANGOLA.—1315: Huambo District, Morro de Sume, $\pm$ 27 km SSE of Nova Lisboa, (–BA), 14 May 1973, *Leach, Cannell & De Sousa 14538* (BM, PRE).

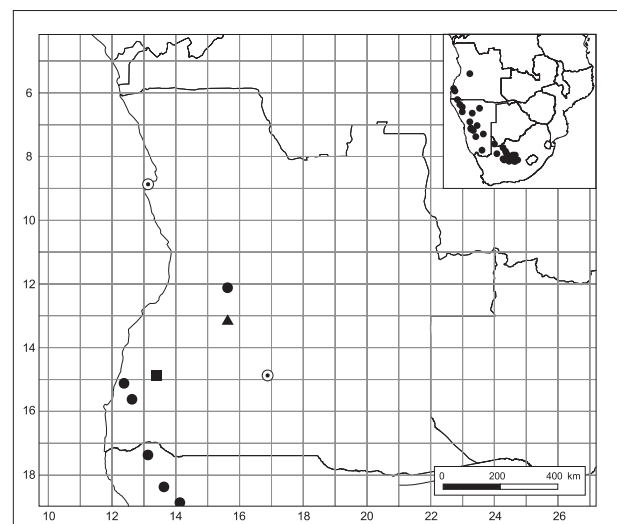


FIGURE 6.— Distribution of *Aloe hereroensis* var. *hereroensis*, ●; *A. lepida*, ▲; *A. mendesii*, ■, and *A. metallica*, ○.

A. littoralis Baker in Transactions of the Linnean Society of London 1: 263 (1878). Type: Angola, near Luanda, Barra do Bengo, 1854, *Welwitsch* 3727 (BM, holo.!; K!, LISU!, iso.-PRE, photo.).

A. rubrolutea Schinz: 39 (1896). Types: Namibia, Rehoboth, *Fleck* 497a; Namibia, !Kuisib, *Fleck* 472; Botswana, Olifantskloof, *Fleck* 263 (Z, syn.).

A. schinzii Baker: 459 (1898). Type: Botswana, Olifantskloof, April 1888, *Schinz* 42 (K, holo.).

Solitary, arborescent plant 2–4 m high. *Stem* unbranched, erect, with persistent dried leaves. *Leaves* densely rosulate, erectly spreading to slightly recurved, pale greyish green with reddish tinge in dry conditions, without spots when mature, few spots on young plants, lanceolate, $\pm$ 600 mm long, 100–130 mm wide at base; margin cartilaginous, yellow, with pungent, red-brown teeth, 3–4 mm long, 10–15 mm apart; leaf exudate drying yellow. *Inflorescence* 1–2 m high, erect, up to 10-branched, lower branches usually rebranched. *Racemes* narrowly cylindrical-acuminate, 300–600 mm long, lax. *Floral bracts* 12–18 $\times$ 5–6 mm. *Pedicels* 6–10 mm long. *Flowers*: perianth pinkish red, yellowish towards tips when mature, with bloom, 27–34 mm long, 6 mm across ovary, enlarging very slightly towards middle, cylindrical and almost straight; outer segments free for 15–17 mm. *Stamens* exerted 1–2 mm. *Style* exerted 2–3 mm. *Flowering time*: July to February, varying according to locality and rainfall.

Diagnostic characters: caulescent, simple-stemmed, solitary plants. Leaves without spots when mature, few spots on young plants. No spines along median line of leaf. Inflorescence branched from low down. Flowers cylindrical, stigma seldom if ever exerted more than 3 mm.

Relationships with other species: closely allied to *Aloe esculenta* (see notes under latter species). *A. littoralis* is included in Section *Pachydendron* (Haw.) Salm-Dyck (Glen & Hardy 2000).

Habitat: usually grows on rocky outcrops in mixed open woodland and grassland. Also on calcrete or sand. Summer rain and very dry, warm to cool winters.

Distribution: Angola (Bengo, Benguela, Cuanza Norte, Cuanza Sul, Huambo, Huila, Luanda, Lunda Norte, Malange, Moxico, Namibe), Botswana, western Mozambique, Namibia, South Africa (Limpopo), southern Zimbabwe (Figure 7).

Illustrations: Reynolds: 317, 318 (1966); Rothmann: 68, 69 (2004).

Additional specimens examined

ANGOLA.—0720: Arredores de Dundo, (–BD), April 1953, *S.c.* 135 (LISC). 0813: Luanda, (–CB), *Exell & Mendonça* 37 (LISC); Luanda, próximo da Corimba, (–CC), 29 August 1961, *Santos* 433 (LISC); Luanda, near Cacucaco, 10 miles [16 km] NE of Luanda, (–CD), 12 July 1959, *Reynolds* 9402 (PRE); Luanda, Viana, Vale do Bengo, (–CD), 23 April 1966, *Teixeira* 10326 (LISC). 0914: Luanda, Cambambe-Dondo, (–CB), 18 August 1931, *Gossweiler* 9633 (LISC); Cuanza Norte, Dondo, Rio Cuanza, (–CB), March 1938, *Gossweiler* 11963 (LISC); Cuanza Norte, Dondo, (–CB), *Gossweiler* 12613 (LISC). 0915: Malange, Cacuso, próximo do salto do Cavallo, (–DB), 15 July 1970, *Raimundo* 327 (LISC); Malange, na picada que vai da Aldeia Formosa para o salto do Cavallo, (–DB), 15 July 1970, *Raimundo, Matos & Figueira* 327 (LISC). 1013: Foz de Cuvo, (–DD), 30 March 1973, *Bamps & Martins* 4342 (LISC). 1113: Cuanza Sul, Gabela, picada para o Pau do Caçador e Gungo a 43 km de Novo

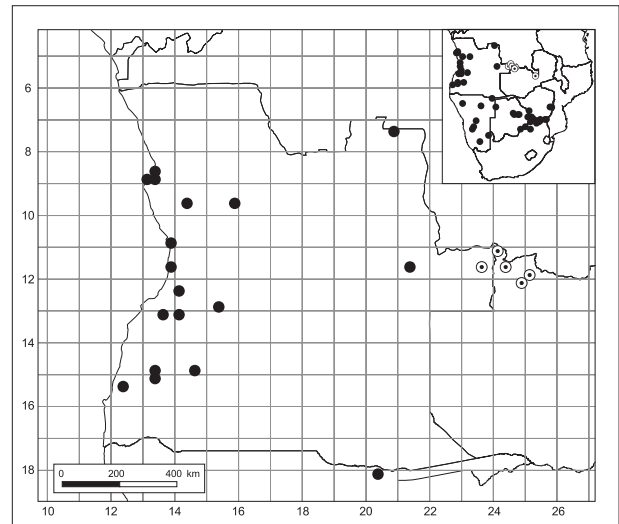


FIGURE 7.— Distribution of *Aloe littoralis*, ●; and *A. milne-redheadii*, ○.

Redondo, (–DB), 19 April 1969, *Teixeira* 11430 (LISC). 1121: Lago Calundo, (–CB), January 1955, *Machado* 358 (LISC). 1214: Lobito, 9 miles [14.5 km] W of Bocoio (Sousa Lara), 49 miles [79 km] E of Lobito, (–AC), June 1959, *Reynolds* 9317 (PRE). 1215: Benguela, Chicala-Calenga, near Sete River, (–CD), 19 June 1940, *Gossweiler* 12598 (LISC). 1313: Benguela, Catengue, (–BA), 29 July 1940, *Gossweiler* 12619 (LISC). 1314: Benguela, près de Caimbambo, (–AA), 17 February 1974, *Dechamps, Murta & Silva* 1095 (LISC). 1413: Serra da Chela, Vila Arriaga, Bibala, (–CD), 12 August 1941, *Gossweiler* 13297 (LISC); Huila, Moçamedes, Bibala, Cacanda, (–CD), 7 May 1960, *Mendes* 4003 (LISC); Sá da Bandeira, Mapunda, (–CD), 16 June 1963, *Santos* 1126 (LISC, LISU), Huila, Sá da Bandeira, Mapunda, (–CD), 16 June 1963, *Santos* 1128 (LISC, LISU); Moçamedes, Vila Arriaga, Montipa, (–CD), *Teixeira & Santos* 3855 (SRGH). 1414: Huila, at Vila Paiva Couceiro (Quipuno), 28 miles [45 km] E of Sá da Bandeira, (–DC), 25 June 1959, *Reynolds* 9267 (PRE). 1512: Moçamedes, 30 km a ocidente do Pico do Azevedo, (–AD), 9 March 1969, *Teixeira* 12888 (LISC). 1513: Huila, 11 km do Jau para Bata Bata, (–AB), 30 February 1961, *Barbosa* 9554 (PRE); Serra da Chela, Tchivinguiro, Humpata, (–AB), 6 October 1941, *Gossweiler* 13346 (LISC). No grid: Cascata do Rio Cuango Muquê, 16 July 1954, *Machado* 200 (LISC).

***A. mendesii* Reynolds** in Journal of South African Botany 30: 31 (1964). Type: Angola, Huila District, Humpata, Tundavala escarpment, 4 July 1963, *Santos & Henriques* 1131 (LISC, holo.!; LISU!, LUAI, PRE!, iso.).

Plants growing pendent on vertical cliff faces. *Stem* usually unbranched, up to 1 m long, pendent, without persistent dried leaves. *Leaves* rosulate at stem apex, hanging downwards, green, obscurely lineate, without spots, ensiform, falcately decurved, 500 $\times$ 70–80 mm; margin narrow cartilaginous edge, with blunt, cartilaginous teeth, 1–2 mm long, 10–15 mm apart. *Inflorescence* up to 0.6 m long, pendent, 3- or 4-branched. *Racemes* cylindrical-acuminate, 100 mm long, arcuate-ascending, dense; buds hidden by imbricate bracts. *Floral bracts* 12 $\times$ 5 mm. *Pedicels* 18–20 mm. *Flowers*: perianth scarlet, 25 mm long, 4 mm across ovary, enlarging towards mouth, narrowing just below mouth, cylindric, slightly ventricose; outer segments free for 20 mm. *Stamens* exerted 2–3 mm. *Style* exerted up to 3 mm. *Flowering time*: April to July.

Diagnostic characters: grows hanging down on cliffs. Leaves broad, unspotted. Branched inflorescence pendent, with only racemes arcuate-ascending. Flowers scarlet. Floral bracts and pedicels relatively long.

Relationships with other species: appears to be closely allied to *Aloe veseyi* Reynolds from Zambia (Reynolds 1966).

Habitat: vertical cliff faces.

Distribution: endemic to southwestern Angola (Huila, Namibe) (Figure 6).

Illustrations: Verdoorn: t. 1764 (1964); Reynolds: 170, 171 (1966).

Notes: this species is sometimes wrongly recorded as occurring in northwestern Namibia (Newton 2001). The species in Namibia with which it is mistaken is the Kaokoland endemic *A. corallina* I. Verd.

Additional specimens examined

ANGOLA.—1413: Huila, Sá da Bandeira, Tundavala, (–CD), October 1967, *Leach* 14015 (PRE); Huila, Lubango, Humpata, Buraco do Bimbe, (–CD), 22 April 1960, *Mendes* 3815 (LISC, para.); Huila, Lubango, Escarpa da Tundavala (serra da Chela), (–CD), 20 May 1964, *Menezes* 1133 (LISC, PRE); Huila, Sá da Bandeira, Humpata, Bimbe, (–CD), 3 May 1963, *Santos* 1109 (LISC, para.).

E.A. metallica Engl. & Gilg in Warburg, Kunene-Zambesi Expedition: 191 (1903). Type: Angola, Bié District, near Cuchi, above Capulo, 4 May 1900, *Baum* 891 (B, holo.!–LISC, photo!).

Acaulescent or stem short; rosettes single. *Leaves* densely rosulate, erectly spreading, bluish grey with metallic sheen (sometimes lost, especially in cultivation), without spots or markings, broadly lanceolate-attenuate, 250–400 mm long, 70–90 mm wide at base; margin slightly reddish brown, horny, with pungent, reddish brown teeth, 2–3 mm long, 10–20 mm apart. *Inflorescence* up to 1.2 m high, erect, sparsely branched. *Racemes* narrowly cylindrical-acuminate, terminal raceme 350 mm long, dense; buds hidden by large, densely imbricate bracts. *Floral bracts* 18–20 × 8 mm. *Pedicels* 8 mm long. *Flowers:* perianth reddish pink, 32 mm long, 7 mm across ovary, enlarging slightly from middle towards mouth, slightly compressed-trigonal; outer segments free for 13 mm. *Stamens* exerted up to 2 mm. *Style* exerted up to 3 mm. *Flowering time:* April to July.

Diagnostic characters: bracts long, white, prominently nerved. Apical buds of racemes at first covered by densely imbricate bracts.

Relationships with other species: Reynolds (1966) placed *Aloe metallica* in his Group 9. It keys out with *A. massawana* Reynolds (now a synonym of *A. eumasawana* S. Carter & M.G. Gilbert) from eastern Africa, *A. vacillans* Forssk. and *A. officinalis* Forssk. from Yemen.

Habitat: top of rocky gorge, between high sandstone rocks.

Distribution: endemic to Angola (Cuando-Cubango, Luanda) (Figure 6).

Illustration: Reynolds: 152 (1966).

Additional specimens examined

ANGOLA.—0713: Luanda, estrada da Corimba, (–CC), 7 March 1971, *Henriques* 1329 (LISC, LISU). 1416: Cuchi River Gorge, (–DD), *Leach* 13850 (PRE); Menongue, Cuchi, Cáquima, Rio Cuchi, (–DD), 3 April 1960, *Mendes* 3444 (LISC), 16 July 1964, *Reynolds* 10104 (LISC, PRE).

A. milne-redheadii Christian in Journal of South African Botany 6: 177 (1940a). Type: Angola, Moxico District, between River Zambezi and River Lusavo, *Milne-Redhead* 4253 ex *Christian* 926 (SRGH, holo.; K, iso.).

Acaulescent or with short stem, suckering to form dense clumps. *Leaves* densely rosulate, erect and curving inward, greyish green to brownish green, becoming slightly reddish in dry conditions, densely white-spotted on both surfaces, spots more copious on lower surface and arranged in transverse bands, ovate-lanceolate, 200–300 mm long, 60–80 mm wide at base; margin cartilaginous, with minute, brown-tipped teeth, 2–3 mm long, 10–15 mm apart. *Inflorescence* 0.6–0.9 m high, erect, 1–7-branched. *Raceme* narrowly cylindrical-acuminate, 200–250 mm long, dense. *Floral bracts* 5–6 × 2–3 mm. *Pedicels* 13–18 mm long. *Flowers:* perianth bright coral-red, 28–35 mm long, ± 8 mm across ovary, slightly narrowed above ovary, curved and widening towards mouth, cylindrical-trigonal; outer segments free for 10 mm. *Stamens* exerted 0–1 mm. *Style* exerted 1–2 mm. *Flowering time:* June to July.

Diagnostic characters: racemes short, rather dense. *Pedicels* long. *Leaves* copiously spotted with spots in transverse bands. Plants forming clumps.

Relationships with other species: its nearest ally is *Aloe bukobana* Reynolds from Rwanda, Burundi and Tanzania (Reynolds 1966).

Habitat: ridges of hills.

Distribution: eastern Angola (Moxico), northwestern Zambia (Figure 7).

Illustration: Reynolds: 110 (1966).

Additional specimen examined

ANGOLA.—1123: Moxico District, between River Zambezi and River Lusavo, (–DA), material from type plant, 7 July 1941, *Verdoorn* PRE29568 (PRE).

A. nuttii Baker in Hooker's, Icones plantarum: t. 2513 (1897). Type: Zambia, Fwambo, South of Lake Tanganyika, 1896, *Nutt* s.n.; Zambia, Fwambo, 1894, *Carson* 29 (K, syn.!–PRE, photo!).

A. brunneo-punctata Engl. & Gilg: 189 (1903). Type: Angola, Longa, oberh. Minnesera, 2 February 1900, *Baum* 698 (B, holo.!; BR!, E!, K!, M!, iso.–PRE, photo!).

A. corbisieri De Wild.: 29 (1921). Type: DRC, Katanga, Elisabethville, Welgelegen, 1912, *Corbisier* 623 (BR, syn.!); DRC, Lukafu, February 1900, *Verdick* 417 (BR, syn.!).

A. mketiensis Christian: t. 785 (1940b). Type: Tanzania, Inringa District, Sao Highlands, north of Mketi, 17 June 1938, *Pole Evans & Erens* 795 (PRE24803) (PRE, holo.!).

Grass aloe, growing singly or with 2 or 3 stems, sometimes up to 12 and more tufted stems. *Stems* very short or up to 0.2 m long, erect. *Leaves* rosulate, erectly spreading, sometimes deflexed at about middle, green, upper surface sometimes obscurely lineate, usually with few pale spots near base, lower surface usually copiously spotted near base, spots occasionally spinulose, grass-like and subfleshy, linear, 400–500 mm long, up to 40 mm at dilated base, abruptly narrowed to 15–20 mm, tapering towards apex; margin very narrow, white, with densely crowded, minute, white, soft, cartilaginous teeth, up to 1 mm long. *Inflorescence* 0.6–0.8 m high, erect, unbranched. *Raceme* cylindrical-acuminate, 150–200 mm long, dense; buds entirely covered by large imbricate bracts. *Floral bracts* 15–25 × 10–20 mm. *Pedicels* 25–35 mm long. *Flowers:* perianth coral-pink to orange-red with green tips, 35–42 mm long, 7–9 mm across

ovary, not narrowed above ovary, cylindrical-trigonus, base tapering into pedicel; outer segments free almost to base or for $\frac{3}{4}$ of length. *Stamens* not exerted. *Style* exerted 0–1 mm. *Flowering time*: January to March, depending on locality and rainfall.

Diagnostic characters: leaves grass-like, rosulate. Flowers salmon-pink.

Relationships with other species: its nearest ally is *Aloe buehneri* Baker from Malawi (Reynolds 1966).

Habitat: montane grassland, often on rocky slopes.

Distribution: southeastern Angola (Cuando-Cubango), southern Democratic Republic of the Congo, Malawi, southwestern Tanzania, northern Zambia (Figure 8).

Illustrations: Christian: t. 762 (1940c); Reynolds: 33, 34 (1966); Lane: 9 (2004).

Additional specimens examined

ANGOLA.—1417: Menongue, Vila Serpa Pinto, vale do Rio Cabumbé, (–DB), 15 February 1960, *Mendes* 2575 (LISC). 1517: Menongue, andados 50 km de Caiundo para Vila Serpa Pinto, (–BC), 4 February 1960, *Mendes* 2354 (LISC). 1519: Bié, Menongue, Rio Cuito, Vale do ribeiro Sobi, (–AC), 13 March 1906, *Gossweiler* 4213 (LISC). 1718: Menongue, entre Longa e Vila Serpa Pinto, vale do Luassingua, (–CA), 22 March 1960, *Mendes* 3243 (LISC). No grid: Longa, oberh. Minnesera, 2 February 1900, *Baum* 698 (BM, BR, E, K, M–PRE, photo.); Moxico, between Kangeshi River and Kaboli River, 20 January 1938, *Milne-Redhead* 4260 (K–PRE, photo.).

A. paedogona A.Berger in *Journal of Botany, British and Foreign* 44: 57 (1906). Type: Angola, Malange, June 1903, *Gossweiler* 946 (BM, holo.!, K, iso.!).

Acaulescent, with leaf bases enlarged below ground to form bulb-like swelling; rosettes single, rarely suckering to form small groups. *Leaves* rosulate, usually deciduous, erectly spreading to slightly recurved, green, obscurely lineate, sometimes with few scattered whitish spots, surface smooth, ensiform, 450 × 50–60 mm; margin whitish, cartilaginous, with firm unevenly spaced teeth, 3 mm long, 5–40 mm apart. *Inflorescence* up to 2 m high, erect, 3–5-branched. *Racemes* cylindrical-conical to subcapitate, 70 mm long, dense. *Floral bracts* 15–25 × 4–6 mm. *Pedicels* 25–30 mm long. *Flowers*:

perianth yellow-green, ± 35 mm long, 9–11 mm across ovary, constricted above ovary, forming globose basal swelling, enlarging towards middle, narrowing towards mouth; outer segments free only at tips. *Stamens* not exerted. *Style* exerted up to 2 mm. *Flowering time*: September to April.

Diagnostic characters: underground bulb. Leaves ± 450 × 50–60 mm, with firm teeth of ± 3 mm long. Unusual shape of flowers with globose basal swelling. Floral bracts linear-lanceolate, long-acuminate, 15–25 mm long.

Relationships with other species: Reynolds (1966) considered *Aloe paedogona* to be conspecific with *A. buettneri* together with *A. bulbicaulis*. Carter (1994) stated that the three taxa are morphologically clearly distinct and also separated geographically and therefore does not agree with Reynold's opinion that the three taxa are conspecific.

Habitat: floodplains, woodland, savanna and grassland.

Distribution: Angola (Bié, Huambo, Huíla, Malange), northern Namibia (Figure 8).

Illustrations: as *Aloe buettneri* in Rothmann: 46, 47 (2004).

Additional specimens examined

ANGOLA.—0915: Malange, near Mateti, 20 miles W of Malange, (–BD), 10 April 1960, *Reynolds* 9384 (PRE). 0916: Malange, type locality, (–CB), July 1959, *Reynolds* 9388 (PRE). 1117: Malange, (–DA), 1903, *Almeida* s.n. (LISC); Malange, Capunda, Mulundo, Reserva da Palanca Preta, picada do Luasso, (–BC), 5 August 1965, *Correia* 3013 (LISC); Malange, Capunda, Mulundo, Reserva da Palanca Preta, (–BC), 6 August 1965, *Henriques* 575 (LISC, LISU), 19 August 1965, *Menezes* 1984 (LISC). 1215: Nova Lisboa, 24 miles [38.5 km] E of Balombo, 134 miles [215.5 km] E of Lobito on road to Nova Lisboa, (–AC), 31 March 1960, *Reynolds* 9328 (PRE). 1216: Bié Province, 4 miles [6.5 km] E of Chinguar, about midway between Silva Porto and Nova Lisboa, (–CB), 31 January 1960, *Reynolds* 9234 (PRE). 1217: Bié, between Coimba and Cuanza River, (–CB), *Exell & Mendonça* 1752 (LISC). 1315: Caconda, Cunene River, Cadincololo, (–CC), 27 July 1905, *Gossweiler* 1792 (LISC). 1415: Ganguelas, Dongo, ribeiro Cussaba, (–DA), 1 August 1905, *Gossweiler* 1807 (LISC). 1416: Huíla, Ganguelas, Vila Artur de Paiva, (–AD), 25 January 1960, *Mendes* 2175 (LISC).

A. palmiformis Baker in *Transactions of the Linnean Society of London* 1: 263 (1878). Type: Angola, Huíla District, Morro de Lopolo, April 1860, *Welwitsch* 3726 (BM, holo.!, K!, LISU!, iso.).

Shrubby plants. *Stem* very slender, 1.0–1.5 m long, erect, sparsely branched mostly at base, with persistent dried leaves. *Leaves* rosulate at branch apices, arcuate-ascending-recurved or spreading-recurved, dull green with reddish tinge, lower surface with many small, crowded, pale green almost white spots towards base, narrowly lanceolate-attenuate, up to 300 × 50 mm; sheath lineate, 10 mm long; margin with prominent, pungent, pale brown teeth, 4–5 mm long, 10 mm apart; leaf exudate crusty when dry. *Inflorescence* 0.4–0.5 m high, erect, up to 4-branched, sometimes simple in young plants. *Raceme* cylindrical, slightly acuminate, 100–150 mm long, lax. *Floral bracts* 2–3 × 2 mm. *Pedicels* 13–15 mm long. *Flowers*: perianth rose-scarlet, 30 mm long, 5.5 mm across ovary, slightly enlarging towards mouth, cylindrical-trigonus; outer segments free for 10 mm. *Stamens* exerted up to 1 mm. *Style* exerted up to 2 mm. *Flowering time*: April to June.

Diagnostic characters: stems very slender, usually sparsely branched. Leaves sometimes unspotted on both

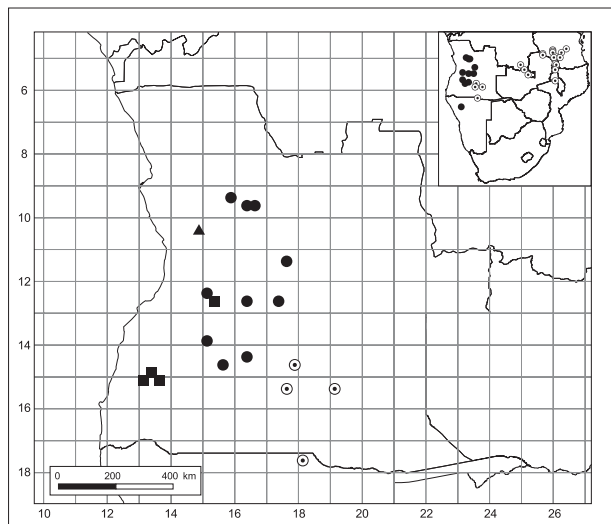


FIGURE 8.—Distribution of *Aloe nuttii*, ○; *A. paedogona*, ●; *A. palmiformis*, ■; and *A. procera*, ▲.

sides, usually copiously spotted on lower surface near base. Marginal teeth prominent. Inflorescence usually 2- or 3-branched, 0.4–0.5 m high.

Relationships with other species: it is closely allied to *Aloe gossweileri* (Reynolds 1966).

Habitat: among standstone rocks in woodland.

Distribution: endemic to Angola (Huambo, Huila, Namibe) (Figure 8).

Illustrations: Reynolds: 354, 355 (1966).

Additional specimens examined

ANGOLA.—1215: Benguela, Capanga, Veva, (–CB), 17 June 1940, Gossweiler 12599 (LISC). 1413: Huila, Lubango, Tundavala, ao km 16, (–CD), 27 April 1971, Borges 119 (LISC, PRE); Huila, Lubango, Humpata, pr. do Perimetro Florestal, (–CD), 15 April 1960, Mendes 3604 (LISC); Huila, Sá da Bandeira, 7 miles [11 km] NE of Humpata, 8 miles [13 km] SW of Sá da Bandeira, (–CD), 29 June 1959, Reynolds 9292 (BM, PRE); Huila, Sá da Bandeira, Humpata, próximo de Bimbe, (–CD), 3 May 1963, Santos 1110 (LISC, LISU); Huila, Sá da Bandeira, Humpata, a 6 km de Sá da Bandeira, (–CD), 3 May 1963, Santos 1112 (LISC, LISU). 1513: Morro de Lopolo, near Huila village, 16 km SE of Sá da Bandeira, (–AA), 27 May 1965, Reynolds 9288 (LISC, PRE); Huila, Serra do Lopolo, pr. Cascata, (–BA), 20 May 1966, Correia 3824 (LISC).

^E*A. procera* L.C. Leach in Journal of South African Botany 40: 117 (1974). Type: Angola, Cuanza Sul District, ± 50 km N of Quibala, 12 July 1972, Leach & Cannell 14617 (LISC, holo.!, BM, LISC!, SRGH, iso.).

Solitary rosettes, erect. Stem short, up to 0.25 m, sometimes acaulescent. Leaves densely rosulate, erectly spreading, very slightly recurved at apex, pale green, obscurely lineate, without spots, ovate-attenuate, apical portion drying out, up to 550 mm long including withered apical portion, 80–95 mm wide; margin narrow, cartilaginous, pale yellow, with orange-brown tipped teeth, 1.5–3.5 mm long, 10–18 mm apart. Inflorescence 2.2–2.75 m high, erect, 9–12-branched, lower branches rebranched. Raceme cylindrical, 250–400 mm long, oblique, lax; buds and flowers secund. Floral bracts 5–6 × ± 4 mm. Pedicels 1.5–5 mm long. Flowers: perianth dull reddish purple, 28–33 mm long, 5–6 mm across ovary, not or only slightly narrowed above ovary, slightly widening at mouth, fairly straight, cylindric-trigonous; outer segments free for 9–11 mm. Stamens slightly exserted. Style exserted up to 6 mm. Flowering time: July to August.

Diagnostic characters: leaves pale green, 80–95 mm wide, apical portion dry and withered. Inflorescence remarkably tall, up to almost 3 m, branched above middle, with long laxly flowered racemes of small purple flowers, subtended by small few-nerved bracts.

Relationships with other species: this species belongs to the group containing *Aloe christianii* from south and central tropical Africa, *A. pretoriensis* from northern South Africa and Zimbabwe and *A. luapulana* L.C. Leach from Zambia, but has its closest affinity with *A. guerrae* (Leach 1974).

Habitat: tall grass in deciduous woodland on steep hillside.

Distribution: endemic to Angola (Cuanza Sul) (Figure 8).

Illustration: Leach: 119 (1974).

Additional specimen examined

ANGOLA.—1014: Cuanza Sul, 50 km N of Quibala, (–BD), 6 August 1972, Leach & Cannell 14617B (PRE).

^E*A. rupicola* Reynolds in Journal of South African Botany 26: 89 (1960). Type: Angola, Bié District, Chingango, rocky hills 3 miles [5 km] S of Chinguar, 19 June 1959, Reynolds 9243 (PRE, holo.!, K!, LUAI, iso.).

Arborescent plant, 2–3 m (sometimes up to 5 m) high. Stem erect, simple or branched at base, 100–120 mm diam., without persistent dried leaves. Leaves densely rosulate, suberectly spreading to spreading, green, obscurely lineate on upper surface, more prominently lineate on lower surface towards base of leaf, lanceolate, apical portion usually drying out, 300–350 mm long plus 100 mm dried apical portion, 60 mm wide; margin with pungent, reddish brown teeth, 4–5 mm long, 10 mm apart; leaf exudate drying pale yellow. Inflorescence 0.7–0.9 m high, erect, 3–5-branched. Racemes cylindrical, 150–180 mm long, dense. Floral bracts ± 9 × 5 mm. Pedicels ± 12 mm long. Flowers: perianth orange-scarlet, 42 mm long, 7 mm across ovary, slightly enlarged above ovary towards mouth, cylindrical-trigonous, slightly clavate; outer segments free for 21 mm. Stamens exserted 2–3 mm. Style exserted up to 3 mm. Flowering time: June to July.

Diagnostic characters: stems averaging 2–3 m, mostly simple or branched from the base. Old dry leaf remains not persistent. Leaves obscurely lineate on upper surface, more prominently lineate on lower surface, especially in lower half. Perianth slightly clavate.

Relationships with other species: its closest ally appears to be *Aloe volkensii* Engl. from eastern Africa (Reynolds 1966).

Habitat: rocky hills.

Distribution: endemic to Angola (Bié) (Figure 9).

Illustrations: Reynolds: 323, 324 (1966).

Notes: this species is only known from the type locality.

^E*A. scorpioides* L.C. Leach in Journal of South African Botany 40: 106 (1974). Type: Angola, Moçâmedes District, near Humbia, towards base of W escarpment of Serra de Chela, April 1973, Leach & Cannell 14654 (LISC, holo.!, BM!, BR, K!, LUA, LUAI, M!, MO!, PRE, SRGH, ZSS, iso.).

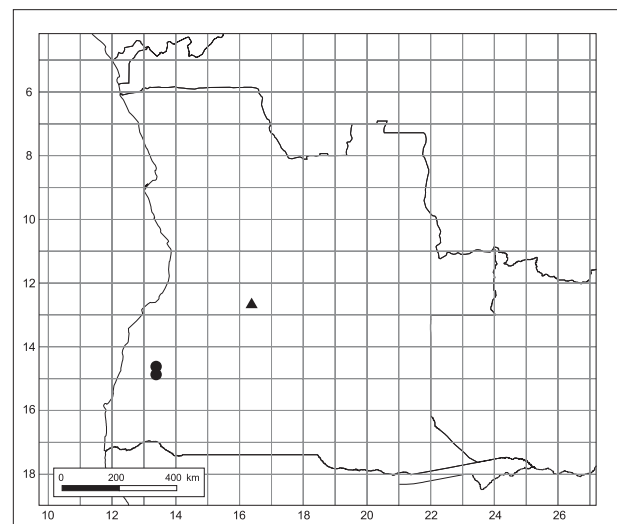


FIGURE 9.— Distribution of *Aloe rupicola*, ▲; and *A. scorpioides*, ●.

Low scrambling shrub, up to 0.5 m high, rarely up to 1 m. *Stem* branching at base and above, slightly divergent, usually widely spreading, only rarely erect, with persistent dried leaves. *Leaves* rosulate at branch apices, more cauline dispersed below, spreading or somewhat recurved, yellowish green, upper surface without spots, lower surface darker, obscurely lineate, rarely with few spots near base, very narrowly ovate-acuminate, up to $300 \times 25\text{--}35$ mm; sheath striate, 10–20 mm long; margin with pungent, yellowish or brownish tipped teeth, somewhat forward-hooked, 2–3 mm long, 10–15 mm apart; leaf exudate crusty when dry. *Inflorescence* ± 0.15 m long, descending at base and curving upwards, simple or 1- or 2-branched. *Raceme* narrowly conical or cylindrical-acuminate, 110–250 mm long, laterals usually shorter, dense. *Floral bracts* $\pm 6.5 \times$ up to 3.5 mm. *Pedicels* 6–10 mm long. *Flowers*: perianth scarlet, yellow-striped with green at base, 21–28 mm long, ± 7 mm across ovary, narrowed above ovary, enlarging towards wide-open mouth, cylindric-trigonous; outer segments free for 8.5–10.0 mm. *Stamens* exserted. *Style* exserted up to 2.5 mm. *Flowering time*: April to May.

Diagnostic characters: plants scrambling and shrubby in habit. Leaves yellow-green, almost invariably immaculate, with small marginal teeth. Inflorescence with very slender peduncle, which is at first usually descending, then arcuately-ascending, with the rather dense, narrow, acuminate racemes held erect. Buds suberect. Flowers curved. Bracts large, prominently nerved, orange-brown.

Relationships with other species: its closest relative seems to be *Aloe palmiformis* Baker (Leach 1974).

Habitat: rocky slopes, often in shade of woodland.

Distribution: endemic to Angola (Huila, Namibe) (Figure 9).

Illustrations: Leach: 107, 108 (1974).

Additional specimen examined

ANGOLA.—1413: Moçâmedes, western slopes of the Serra da Chela, ± 14 miles [22.5 km] W of Sá da Bandeira, (–CB), 21 April 1972, Reynolds 9275 (LISC).

^E**A. vallis** L.C. Leach in Journal of South African Botany 40: 111 (1974). Type: Angola, Huila District, Serra da Chela escarpment, cliffs W of Tchivinguiro, 23 April 1973, Leach & Cannell 14651 (LISC, holo.!; BM!, BR!, K!, LISC!, LUAI, M!, MO!, PRE!, SRGH, WIND, ZSS, iso.).

Shrubby plant, 0.3–0.5 m high. *Stem* branched from base; rosettes tilted to one side, greyish or greenish blue to bluish green. *Leaves* rosulate at branch apices, more widely spaced below, few small, oval or round, whitish spots near base, more spots on lower surface, narrowly ovate-attenuate, $220\text{--}340 \times 40\text{--}50$ mm; sheath copiously spotted; margin narrow, yellowish, with pungent, yellowish, orange- or brown-tipped teeth, 2.0–2.5 mm long, 10–12 mm apart; leaf exudate frothy, drying to opaque, crystalline, yellow crust. *Inflorescence* 0.5–0.6 m, oblique or suberect, simple or divaricately 1-branched. *Racemes* narrowly elongate cylindrical-acuminate, terminal raceme 250–450 mm long, lateral raceme 170–300 mm long, oblique, lax. *Floral bracts* up to 4.5×2.5 mm. *Pedicels* 4.0–4.5 mm long. *Flowers*: perianth bright scarlet, somewhat purplish at apex, mouth becoming

yellowish at maturity, 20–25 mm long, ± 5 mm across ovary, narrowed slightly above ovary, enlarging slightly towards open mouth, slightly curved, cylindric; outer segments free for 4.5–6.0 mm. *Stamens* and *style* not or scarcely exserted up to 1 mm. *Flowering time*: April.

Diagnostic characters: very shrubby plant of relatively dwarf stature, with stem branched from base. Rosettes of grey-blue to blue-green leaves tilted to one side. Inflorescence simple or 1-branched from low down, with narrow acuminate racemes. Short, bright scarlet flowers with outer segments free for only 4.5–6.0 mm carried on relatively short pedicels.

Relationships with other species: it appears to be most closely allied to *Aloe gossweileri* and *A. catengiana* (Leach 1974).

Habitat: cliffs.

Distribution: endemic to Angola (Namibe) (Figure 5).

Illustrations: Leach: 113 (1974).

Notes: this species is only known from the type locality.

^E**A. venenosa** Engl. (insufficiently known sp.) in Botanische Jahrbücher 15: 471 (1893). Type: Angola, Lunda, between Quimbundu and Nyangwe, 20 May 1882, P. Pogge 1460 (B, holo.–LISC, photo!).

Growth form unknown. *Leaves* 350×70 mm; margins with teeth, 6–7 mm long. Inflorescence copiously paniculate. *Raceme* 250–350 mm long. *Pedicels* 25 mm long. *Flowers*: perianth pale red, 27–30 mm long. *Flowering time*: May.

Relationships with other species: unknown.

Distribution: endemic to Angola (Lunda Norte or Lunda Sul).

Notes: this species has not been located since the type specimen was collected by Pogge in May 1882. The true identity of this species, therefore, remains a mystery. Furthermore, the type locality is extremely vague: Quimbundu is in northeastern Angola, whereas Nyangwe is in the eastern Democratic Republic of the Congo. It is therefore possible that this species was not collected in Angola, but in the Democratic Republic of the Congo.

A. zebrina Baker in Transactions of the Linnean Society of London 1: 264 (1878). Type: Angola, Loanda District, Barra do Bengo, Quicuxe towards Cacauco, July 1854, Welwitsch 3721 designated by Reynolds (1966) (LISU, lecto.!; BM!, G!, K!, islecto.–LISC, photo!).

A. platyphylla Baker: 264 (1878). Type: Angola, Pungo Andongo, 1879, Welwitsch 3722 (K, lecto.!; BM, G!, LISU!, islecto.).

A. constricta Baker: 168 (1880). Type: Mozambique, near Sena, 8 April 1860, Kirk 34 (K, holo.).

A. lugardiana Baker: 135 (1901). Type: Botswana, Botletle River, 30 June 1897, Lugard 2 (K, holo.).

A. baumii Engl. & Gilg: 191 (1903). Type: Angola, Chirumbu, 14 October 1899, Baum 275 (B, holo.; E, iso.).

A. bamangwatensis Schönland: 122 (1904). Type: Botswana, Palapye Road, March 1904, Schönland 1656 (GRA, holo.; PRE, iso.).

Acaulescent; rosettes sometimes solitary or usually suckering to form groups. *Leaves* densely rosulate, spreading, dull green, upper surface with transverse bands of conspicuous, whitish, oblong spots, lower surface usually obscurely or copiously spotted, lanceolate, usually dried

and twisted at apex, 150–350 mm long, 60–70 mm wide at base; margin with stout, pungent, red-brown teeth, 4–7 mm long, 10–15 mm apart; leaf exudate yellowish, drying purplish or orange. *Inflorescence* 0.75–2 m high, erect, 4–12-branched, lower branches often rebranching. *Racemes* narrowly cylindrical-acuminate, 300–400 mm long, very lax. *Floral bracts* 6–15 × 2–3 mm. *Pedicels* 6–15 mm long. *Flowers*: perianth dull red to pinkish red or coral-coloured with paler segment margins, 25–35 mm long, basally inflated to 7–9 mm across ovary, abruptly constricted just above ovary, widening towards mouth, slightly decurved, cylindrical-trigonus; outer segments free for 7–11 mm. *Stamens* exerted 1–2 mm. *Style* exerted up to 2 mm. *Flowering time*: variable, (November) February to April (May), or June to July, depending on the locality.

Diagnostic characters: spotted aloe. Upper leaf surface always conspicuously spotted, spotting on lower surface varies. Very laxly flowered racemes, 300–400 mm long; pedicels 6–15 mm long; perianth averaging 30 mm.

Relationships with other species: *Aloe zebrina* belongs to the Section *Pictae* Salm-Dyck or maculate aloes (Glen & Hardy 2000).

Habitat: variety of veld types and soil, mostly grassland and thickets on dry hills.

Distribution: Angola (Bengo, Cuando-Cubango, Cuanza Sul, Cunene, Huambo, Huila, Luanda, Lunda Sul, Malange, Moxico), Botswana, western Mozambique, Malawi, northern Namibia, South Africa (North-West), Zambia, Zimbabwe (Figure 10).

Illustrations: Reynolds: 90 (1966); Rothmann: 94, 95 (2004).

Additional specimens examined

ANGOLA.—0813: Luanda, entre a foz do Dande e a estrada de Caxito, (–AD), 18 July 1964, *Barbosa 10831, 10832* (LISC); Luanda, Quicuxe, (–BD), *Welwitsch 3720, 3724 & 3725* (K, LISU); Luanda, Caxito, praia de S. Tiago a caminho do Dande, (–CB), 8 May 1958, *Monteiro, Santos & Murta 119* (LISC, LISU); Luanda, near Cac-uaco, 10 miles [16 km] NE of Luanda, (–CD), 12 July 1959, *Reynolds 9406* (PRE); Luanda, Icola e Bengo, near Dande River, (–DA), June 1944, *Gossweiler 13299* (LISC). 0817: Malange, Cambo, Montalegre, (–CC), 27 May 1948, *Rocha 75* (LISC). 0915: Cuanza Norte, Catete, (–BB), 1930, *Gossweiler 9210* (LISC); Pungo Andongo, (–DA), 1879,

Welwitsch 3722 (G, K). 0920: Lunda, near Vila Henrique de Carvalho, (–CA), 22 April 1937, *Exell & Mendonça 921* (LISC); Lunda, Dala, (–CA), 25 April 1937, *Exell & Mendonça 1134* (LISC). 1013: Cuanza Sul, Porto Amboim, estrada S. Filipe-Porto Amboim, a 10 km de S. Filipe, (–DB), 27 April 1967, *Teixeira 11553* (LISC). 1215: Huambo, Nova Lisboa, Chianga, (–DB), 1 June 1971, *Fernando 4* (LISC). 1320: Moxico, (–BA), *Exell & Mendonça 1662* (LISC). 1413: Huila, Sá da Bandeira, Hoque, (–DB), 2 June 1966, *Henriques 1022* (LISC, LISU); Huila, Lubango, Sá da Bandeira, arredores, próximo da escola do Marquês, (–DC), 7 March 1972, *Couto 192* (LISC); Huila, Sá da Bandeira, Vio, (–DC), 4 May 1965, *Henriques 378* (LISC, LISU). 1417: Menongue, entre Cuchi e Vila Serpa Pinto, vale do Luassenha, (–CA), 4 April 1960, *Mendes 3460* (LISC). 1418: Cuito-Cuanavale, andados 40 km de Longa para Cuango, (–BD), 18 March 1960, *Mendes 3175* (LISC). 1513: Huila, Humpata, Tchivinguiro, (–AB), 24 April 1972, *Menezes 4087* (LISC); Huila, Lubango, ao km 17 da estrada para a Chibia, (–BA), 24 April 1965, *Menezes 1590* (LISC); Huila, próximo da Missão Católica, (–BA), 10 February 1956, *Santos 182* (LISC). 1515: Ganguelas, entre os Rios Cubango e Cunene, Rio Oxo, (–BA), 4 August 1905, *Gossweiler 1834a* (LISC). 1516: Menongue, Cuito, vale de Sobi, (–BD), 15 March 1906, *Gossweiler 3704* (LISC). 1519: Cuando-Cubango, Cuito-Cuanavale, sede, (–AA), July 1967, *Pereira s.n.* (LISC). 1614: Roçadas, Centro de Estudos do Cunene, (–DD), 27 March 1970, *Silva 3151* (LISC). 1714: top of Ruacanã Falls, on Angolan side, (–AC), *Rycroft 2435* (NBG). No grid: Moxico, S of Luhanda River, 15 January 1938, *Milne-Redhead 4146* (K–PRE, photo.).

ACKNOWLEDGEMENTS

The authors would like to thank: Ms Hester Steyn, Data Management Unit, SANBI, for the distribution maps; Mr Steve Cafferty, for providing digital images of some BM specimens; two referees for suggesting improvements to the manuscript.

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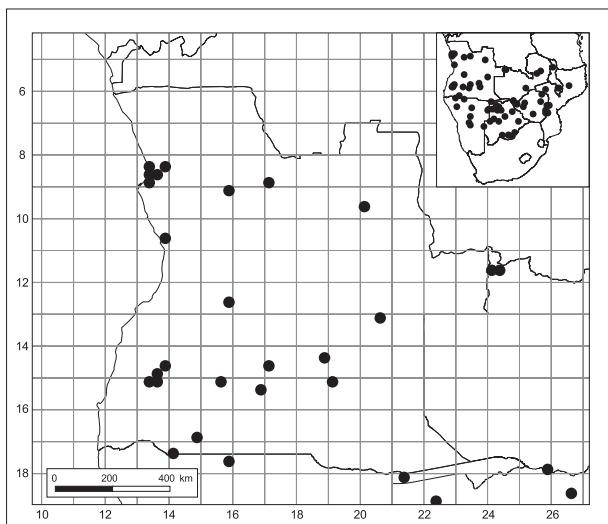


FIGURE 10.— Distribution of *Aloe zebrina*.

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Three new species of *Gladiolus* (Iridaceae) from South Africa, a major range extension for *G. rubellus* and taxonomic notes for the genus in southern and tropical Africa

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Keywords: *Gladiolus* L., Iridaceae, Namibia, new species, South Africa, Tanzania, taxonomy

ABSTRACT

Three new species of *Gladiolus* L. are described from South Africa. *G. dolichosiphon* is the second known member of series *Blandus* from the mountains of the Little Karoo in Western Cape, and is distinguished from other members of the long-tubed, pink-flowered *G. carneus* complex by its 5 or 6 linear leaves, creamy pink to salmon flowers with a tube 30–50 mm long and longer than the dorsal tepal, and its late summer flowering. *G. karoocicus* from the Klein Roggeveld and the northern foothills of the Witteberg, is a spring-flowering species allied to *G. permeabilis* but has bright, canary-yellow flowers with the lower part of the lower tepals involute and conspicuously auriculate. *G. reginae* is an edaphic endemic of the Sekhukhuneland Centre of Floristic Endemism in Mpumalanga, and flowers in autumn. It is evidently a glabrous member of section *Densiflorus* series *Scabridus*, distinguished by its long-tubed flowers, streaked with red on the lower tepals and blotched with red in the throat. Anomalously, however, it has the tubular inner bracts and large capsules diagnostic of section *Ophiolyza* series *Oppositiflorus*. A re-examination of the morphology suggests that series *Scabridus* is better placed in section *Ophiolyza* and a slightly revised classification of *Gladiolus* in southern Africa is proposed. We also propose the replacement name *G. sulcatus* for the Tanzanian species, *G. sulcatus* Goldblatt, a later homonym of *G. sulcatus* Lam. Finally, a recent sighting of what appears to be *G. rubellus* from northern Namibia constitutes the first record of this species in the country and a major range extension from its previous known occurrence in southeastern Botswana.

INTRODUCTION

Gladiolus L., now including some 262 species, is the largest genus of Iridaceae subfamily Crocoideae. It is also the largest genus of Iridaceae in Africa, where 168 species are now known from southern Africa, 82 species from tropical Africa, eight in Madagascar, and a scant 10 in Eurasia. The genus is taxonomically well researched, and recent monographs exist for Madagascar (Goldblatt 1989), tropical Africa–Arabia (Goldblatt 1996), and southern Africa (Goldblatt & Manning 1998). New species continue to be discovered, however, and two have since been added to the genus from southern Africa (Manning *et al.* 1999), another from the Democratic Republic of Congo (Geerinck 2001) and two more have been recognized from Zimbabwe and Mozambique (Goldblatt 2008). Here we describe a further three species from South Africa. *Gladiolus reginae* Goldblatt & J.C.Manning from northwestern Mpumalanga was discovered during a botanical survey of the Steelpoort River Valley, which transects the Sekhukhuneland Centre of Floristic Endemism (Van Wyk & Smith 2001), a region that is still poorly explored botanically. This interesting species is evidently a member of series *Scabridus* (currently placed somewhat uncomfortably at the end of section *Densiflorus* in the classification of the southern African species) but it displays the critical characteristics of section *Ophiolyza*. As a result, we have reassessed the taxonomic position of series *Scabridus* within the genus. A second species, *G. karoocicus* Goldblatt & J.C.Manning of section *Hebea*, from the Western Karoo, was discovered in the spring of 2006, a year of unusually ample rainfall in this semi-arid winter rainfall zone. A third new species, *G.*

dolichosiphon Goldblatt & J.C.Manning, from the mountains of the Little Karoo in Western Cape, was collected in early 2008, although a previously unplaced collection was made two decades earlier.

In addition to describing these new species, we take this opportunity to provide a new name for the Tanzanian *Gladiolus sulcatus* Goldblatt. After examining the checklist of Iridaceae being prepared for the *World checklist of selected plant families* (R. Govaerts pers. comm. 2007), we have learned that the name is a later homonym, and therefore illegitimate. Finally, a recent collecting trip to northwestern Namibia produced what is evidently a new record for that country of *G. rubellus* Goldblatt, previously thought to be endemic to southeastern Botswana.

***Gladiolus dolichosiphon* Goldblatt & J.C.Manning, sp. nov. (section *Blandus*)**

Plantae 200–400 mm altae, cormo subgloboso 10–15 mm diam., tunicis externis aetate in fibras molles solutis, cataphyllis supra terram purpurascensibus obscure viridibus vel albis maculatis, foliis 6 vel 7, inferioribus 3 basalibus grandioribus laminibus linearibus ad anguste ensiformibus 1.5–4.0(–6.5) mm latis marginibus hyalinis foliis caulibus sine laminis, caule simplici vel 1-ramoso, spica ad basem inflexa inclinata 4- vel 5-(ad 7-)flora, ramis 1- vel 2-floris, bractea externa subacuta vel infime attenuata 20–30(–35) mm, interna subacuta ad apicem indivisa, floribus pallide cremeis vel salmoneis inodoris, tepalis inferioribus maculis pallidis medianis circumscriptione atrorubro praeditis, tubo perianthii cylindrico (30–)40–55 mm longo, tepalis inaequalibus lanceolatis dorsalibus 30–40 × 15–17 mm prorsum supra staminibus arcuatis, lateralibus superioribus 25–28 × 12–14 mm, inferioribus tribus prorsum extensis basi ± 2 mm connatis, 20–25 × 4–5 mm, filamentis 16–20 mm longis, antheris 8–9 mm longis, stylo arcuato ramis 8–9 mm longis.

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MS. received: 2008–06–02.



FIGURE 1.— *Gladiolus dolichosiphon*, Schutte & Vlok 941. Photographer: Jan Vlok.

TYPE.—Western Cape, 3321 (Ladismith): Rooiberg, south of track between Rooiberg Pass and Bailey's Peak, (–DB), 7–23 February 2008, A.L. Schutte & J. Vlok 941 (NBG, holo.; K, MO, iso.).

Plants 200–400 mm. *Corm* subglobose, 10–15 mm diam.; outer tunics decaying into soft fibres, pale greyish brown. *Stem* inclined outward above basal leaves, unbranched or with a small lateral branch from axil of one or both uppermost leaves, 1–2 mm diam. below main spike. *Cataphylls* flushed purple above ground and obscurely mottled with green or white. *Leaves* 6 or 7, lower 3 basal and largest, reaching or shortly exceeding spike; blades linear to narrowly sword-shaped, 1.5–4.0 (–6.5) mm wide, midrib slightly thickened and margins hyaline; upper 2 cauline leaves without blades, sometimes subtended by a lateral branch each, margins open to base. *Spike* flexed at base, inclined, weakly flexuose, 4- or 5(–7)-flowered, subsecund, lateral branches 1- or 2-flowered; bracts foliose, outer subacute or lower attenuate, 20–30 (–35) mm, green flushed purple distally, inner slightly shorter or up to two thirds as long, subacute and not forked apically. *Flowers* pale creamy or salmon pink, lower three tepals each with a pale lozenge-shaped median mark outlined in dark red, unscented; perianth tube cylindric, expanded in upper 10 mm, straight or arched distally, (30–)40–55 mm long; tepals unequal, lanceolate, dorsal largest, 30–40 × 15–17 mm, arching forward over stamens and curved upwards distally, upper laterals 25–28 × 12–14 mm, extending forward and curving outward in distal third to half, lower three tepals basally fused for ± 2 mm, narrowly lanceolate, 20–25 × 4–5 mm, in profile shorter than upper tepals. *Filaments* 16–20 mm long, exerted 10–14 mm from tube; anthers 8–9 mm long, purple with cream-coloured pollen. *Ovary* ovoid, ± 5 mm long; style arching beneath dorsal tepal, dividing just before or just beyond anther apices, branches 5–6 mm long. *Capsule* and *seeds* unknown. *Flowering time*: late January to mid-February. Figure 1.

Distribution and ecology: known from two collections from the mountains around Ladismith in the western Little Karoo (Figure 2), where it has been recorded from the top of the Klein Swartberg at an altitude of 1 900 m and from the Rooiberg at over 1 300 m. Plants occur on cooler south-facing slopes in seasonally wet situations, on rocky outcrops or along kloofs. On both occasions *Gladiolus dolichosiphon* was collected on trips that had been undertaken in response to fires that had occurred the preceding summer and while it, like many *Gladiolus* species, evidently flowers well after fire, it is probably not a true pyrophile.

The long-tubed, pink flowers with red markings on the lower tepals, are similar to several other *Gladiolus* species, as well as other Iridaceae, that are adapted to

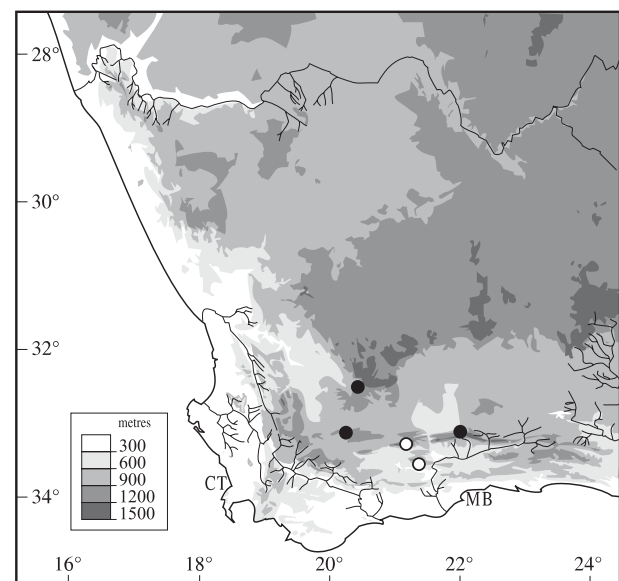


FIGURE 2.—Known distribution of *Gladiolus dolichosiphon*, ○; *G. karooicus*, ●.

pollination by long-proboscid flies in the families Tabanidae and/or Nemestrinidae (Goldblatt & Manning 1999) and there is no doubt that *G. dolichosiphon* is likewise adapted to this pollination system.

Gladiolus dolichosiphon was first collected in February 1986 on the Klein Swartberg by ecologist Jan Vlok while checking on the condition of plants of *Protea pruinosa* after a fire the previous year. This puzzling collection could not be identified, however, and was not included by Goldblatt & Manning (1998) in their revision of the genus in southern Africa. In February 2008, Jan Vlok, accompanied by AnneLise Vlok and Willem Wagenaar from CapeNature, encountered a population of *Gladiolus* in flower on the Rooiberg during a biodiversity survey of the mountain. Suspecting that it was of interest, they collected ample material and photographed the flowers. From this it was clear that the plants represented an undescribed species and further investigation in the herbarium revealed the earlier collection from the Klein Swartberg, which is undoubtedly the same species.

Diagnosis and relationships: the basal fan of narrowly lanceolate leaves and spike of relatively large, long-tubed, pink flowers with median lozenge-shaped markings on the lower three tepals, place *Gladiolus dolichosiphon* among the species of section *Blandus* series *Blandus*. Centred on the variable *Gladiolus carneus* Delaroché, series *Blandus* currently includes 13 species endemic to the mountains of the southwestern Cape, making *G. dolichosiphon* the fourteenth member of the alliance and one of just two that are known from the inland mountains of the Little Karoo. The other Little Karoo species, *G. aquamontanus* Goldblatt & Vlok, is another discovery of Jan Vlok's and this hydrophyte is restricted to the Great Swartberg, where it grows in perennial streams and on wet cliffs.

The relationships between the nine members of the cream- or pink-flowered *Gladiolus carneus* complex are poorly understood. Members of the alliance are distinguished primarily on the relative lengths of the perianth tube and tepals, the proportions of the upper and lower

tepals, and on flowering time and geographical distribution (Goldblatt & Manning 1998) (Table 1).

In its narrow, linear leaves and creamy pink or pale salmon flowers with the tube longer than the dorsal tepal, and the lower tepals with median, lozenge-shaped markings, *Gladiolus dolichosiphon* has a marked similarity to *G. bilineatus*, a local endemic to the southern foothills of the Langeberg, where it occurs mainly in a narrow band along the renosterveld-fynbos transition, and flowers in autumn, in March and April. *G. bilineatus* has just three leaves, usually only the lower one or two with a well-developed blade, 6–8 mm wide, and flowers with a perianth tube 50–70 mm long. *G. dolichosiphon*, from the interior Little Karoo mountains on seasonally moist slopes at high altitude in fynbos, flowers in late summer, in February. Plants have 6 or 7 linear leaves with blades mostly less than 5 mm wide, and a perianth tube 30–55 mm long. These differences in foliage, flower morphology, ecology and distribution are all significant in the context of species delimitation in the *G. carneus* complex.

Etymology: Greek *dolicho*, long; *tubus*, tube, referring to the long perianth tube.

Other material seen

WESTERN CAPE.—3321 (Ladismith): top of Klein Swartberg Mountains, next to Besemfontein track, (–AD), 3 February 1986, Vlok 1407 (NBG).

***Gladiolus karooicus* Goldblatt & J.C.Manning, sp. nov. (section *Hebea*)**

Plantae 150–500 mm altae, cormo conico 25 × 15 mm, foliis usitate 4 laminis linearibus ± 2 mm latis, folio caulino vaginato, caule simplici vel 1–2-ramoso, spica 2- ad 5-flora, bracteis 20–25 mm longis, floribus bilabiatis flavis perodoratis, tubo perianthii subcylindrico ± 12 mm longo, tepali inaequalibus, dorsalibus ± 25 × 10 mm arcuatis, tepalis lateralibus superioribus erectis, tepalis lateralibus inferioribus 12 × 4 mm in dimidio inferiore marginibus incurvis tubum calcariformem formantibus, filamentis ± 15 mm longis 10 mm ex tubo exsertis, antheris ± 8 mm longis, stylo arcuato ramis ± 2.5 mm longis.

TABLE 1.—Selected characteristics of members of *Gladiolus carneus* complex. Distribution data follows centres of endemism in Goldblatt & Manning (2000)

	<i>carneus</i>	<i>pappei</i>	<i>geardii</i>	<i>aquamontanus</i>	<i>undulatus</i>	<i>angustus</i>	<i>buckerveldii</i>	<i>bilineatus</i>	<i>dolichosiphon</i>
Corm	developed	developed	developed	vestigial	developed	developed	poorly developed	developed	developed
Leaf number	4 or 5	3 or 4(5)	7–9	(4)5 or 6	4 or 5	4 or 5	5 or 6	3	6 or 7
Leaf width (mm)	(2)–6–14(–19)	1.6–3.0	14–28	8–15	5–12	(3)–5–10	25–35	6–8	1.5–4.0(–6.5)
Perianth colour	white to pink	pink	pinkish purple	pale mauve-pink	pinkish cream-coloured to greenish	cream-coloured to pale yellow	cream-coloured to pale greenish	creamy pink to pale salmon	creamy pink or salmon
Tube length (mm)	(15)–25–38(–45)	30–35	30–40	(25)–34–40	52–75	(45)–60–110	45–50	50–70	(30)–40–55
Dorsal tepal length (mm)	28–40(–50)	26–30	40–55	30–35	40–50	32–40	28–32	± 23	30–40
Tube:dorsal tepal	≤	≥	<	≥	>	>	>	>	>
Tepal shape	lanceolate	lanceolate	lanceolate	lanceolate	attenuate	lanceolate	lanceolate	lanceolate	lanceolate
Distribution	NW, SW, LB, SE	SW	SE	KM	NW, SW	NW, SW	NW	LB	KM
Flowering time	Oct.–Nov. (Dec.)	Oct.–Dec.	Nov.–Dec.	Nov.–Dec.	Nov.–Dec.	Oct.–Nov.	Dec.–Jan.	Mar.–Apr.	Feb.

TYPE.—Northern Cape, 3320 (Sutherland): Klein Roggeveld, Komsberg Pass, along seasonal stream in damp gully, in shaly gravel, (–DA), 8 September 2006, Goldblatt & Porter 12804 (NBG, holo.; K, MO, PRE, iso.).

Plants 150–500 mm high. *Corm* conical, 25×15 mm; outer corm tunics brown and papery, decaying below into fine to medium-textured fibres. *Stem* suberect, or inclined, flexed outward above sheath of third leaf, simple or with one or occasionally two branches. *Cataphylls* pale and membranous, uppermost reaching shortly above ground and then dull purple. *Leaves* usually 4, more if plants branched, lower 3 with expanded blades, lower 2 longest and reaching at least to base of spike or shortly exceeding it; blades linear, ± 2 mm wide, firm-textured, slightly twisted, midrib moderately thickened, margins evidently not thickened; cauline leaf or leaves short and largely sheathing. *Spike* inclined $\pm$ flexuose, 2–5-flowered; bracts grey-green, sometimes flushed purplish above, often dry and pale near apices, outer 20–25 mm long, inner two thirds to almost as long as outer, acute, not forked at tip. *Flowers* yellow, dorsal and upper laterals flushed and veined grey-purple outside, lower laterals deep yellow in proximal half and turning dull purple on fading, sweetly violet-scented; perianth tube subcylindric, slightly wider near apex, ± 12 mm long; tepals unequal, all narrowed below into claws, lanceolate, dorsal largest, $\pm 25 \times 10$ mm, arched and hooded over stamens, tip curving upward, upper laterals erect, distal halves arching over dorsal tepal, adaxial margins often touching one another, $\pm 25 \times 7$ mm, windowed between lower halves of dorsal and upper lateral tepals, lower 3 tepals joined to upper laterals for ± 2 mm and to each other for ± 3 mm, lower laterals with erect claws ± 1.5 mm long, limbs horizontal, $\pm 12 \times 4$ mm, expanded distally, margins of proximal half involute to form tube extending backward as auricles, lower median $\pm 15 \times 8$ mm long, arching downward in distal third. *Filaments* unilateral and contiguous, arched under dorsal tepal, ± 15 mm long, exserted 10 mm from tube; anthers ± 8 mm long, parallel and contiguous, light purple; pollen whitish. *Ovary* oblong, ± 5 mm long; style arching over stamens, dividing opposite upper third of anthers, branches ± 2.5 mm long, not or barely exceeding anthers. *Cap-sules* obovoid and rounded apically or ellipsoid, 15–20 mm long. *Seeds* ovate, $5\text{--}7 \times 4\text{--}5$ mm, broadly winged, translucent golden brown, with dark seed body ± 2 mm diam. *Flowering time*: mid-August to mid-September. Figure 3.

Distribution and ecology: *Gladiolus karoocicus* is restricted to the Klein Roggeveld and nearby foothills of the Witteberg (Figure 2). The type collection was made in the Komsberg, the scarp separating the high Roggeveld from the Klein Roggeveld but the species has also been recorded from the northern foothills of the Witteberg at Memorial, west of Matjiesfontein, and from near Prince Albert and the foot of the Great Swartberg. It is mostly encountered in damp gullies and along seasonal streams in gravelly, decomposed shale and tillite, among grass clumps and low shrubs. *G. karoocicus* occurs sympatrically with the common and widespread *G. venustus*, also section *Hebea*, which favours drier, more exposed sites. The bright yellow flowers, moderately long peri-

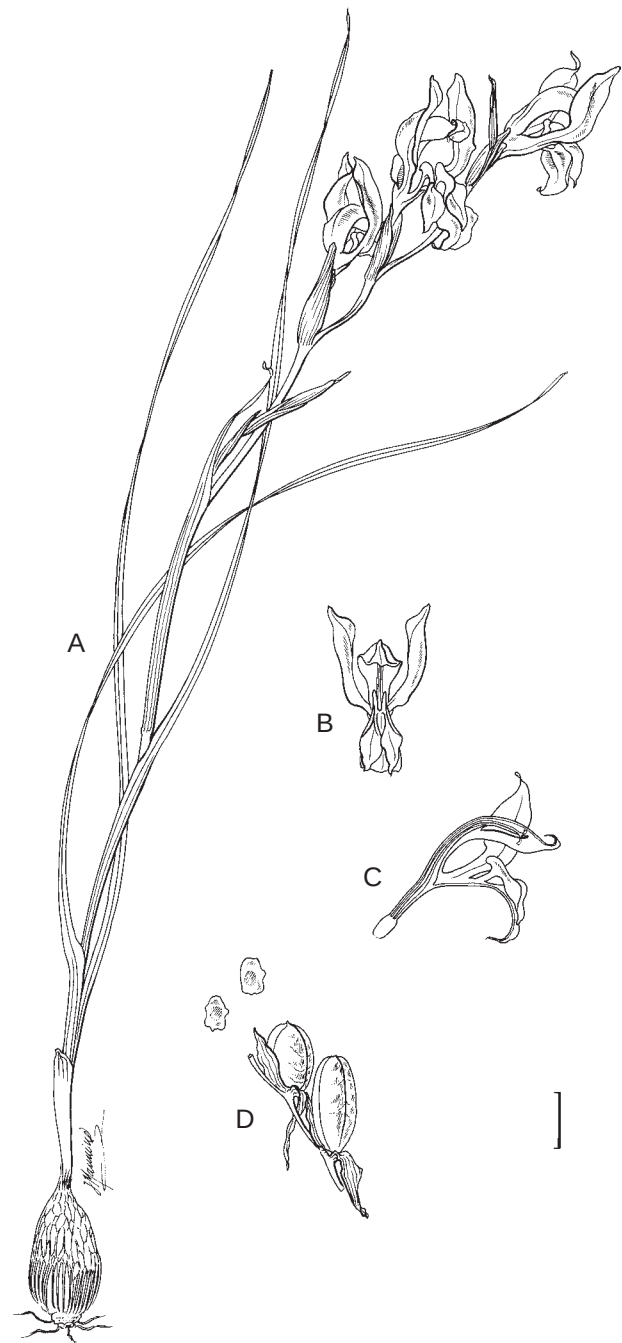


FIGURE 3.—*Gladiolus karoocicus*, Goldblatt & Porter 12804 (NBG). A, flowering plant; B, flower front view; C, half flower; D, capsules and seed. Scale bar: 10 mm. Artist: John Manning.

anth tube, and sweet floral scent suggest that the species is pollinated by long-tongued bees.

In a remarkable coincidence, *Gladiolus karoocicus* was independently discovered by three different parties in the spring of 2006. This was a year of unusually good rains for the western Karoo and it is likely that this attracted botanical collectors to the region as well as encouraging good flowering in the species.

Diagnosis and relationships: *Gladiolus karoocicus* has the unusually narrow, linear leaves without thickened margins, clawed tepals, and distinctive dark seed body characteristic of section *Hebea* (Goldblatt & Manning 1998) and there is no doubt that it should be placed here.

Within section *Hebea*, the soft-textured corm tunics and ellipsoid capsules closely resemble those of members of series *Permeabilis* and on this basis we conclude that *G. karooicus* is probably immediately allied to the small group of species that includes *G. permeabilis*, *G. stellatus* and *G. wilsonii*, comprising the members of the alliance that occur in the winter rainfall zone of southern Africa. *G. karooicus* is distinctive in series *Permeabilis* on account of its bright yellow flowers with geniculate lower tepals that are involute and tubular in the basal half of the blades, with conspicuous auricles above the claw. In *G. permeabilis* and *G. wilsonii* the lower tepals are $\pm$ recurved and although slightly canaliculate, they are evenly narrowed towards the claw and not at all auriculate. In addition, the flower colour is generally dull brownish or lilac, or white. *G. stellatus* has very distinctive, stellate, actinomorphic flowers.

The curiously constructed flowers of *G. karooicus* are remarkably similar to those of *G. venustus* (series *Deserticola*, also section *Hebea*) in their sharply flexed, auriculate lower tepals but the members of this species group share derived woody, clawed corm tunics, a scalloped flower spike, and distinctive, squat, barrel-shaped, apically retuse capsules. In addition, the seed body in series *Deserticola* is brown and not black. The floral similarities between *G. karooicus* and *G. venustus* are thus evidently the result of convergence, possibly the result of pollinator-driven selection. When not in fruit, the two species are separated by the differences in their corm tunics, which are soft in *G. karooicus* and woody in *G. venustus*, and by differences in the orientation of the upper lateral tepals. In *G. venustus* the upper laterals are suberect from the base and not significantly fused to the lower tepals, whereas in *G. karooicus* the upper laterals are fused to the lower tepals for $\pm$ 2 mm and thus horizontal in this basal portion, but abruptly suberect in the distal, free portion, resulting in the presence of the characteristic window between the upper lateral tepals and the lower tepals.

Etymology: *karooicus*, from the karoo, the semi-arid and arid interior part of South Africa.

Other material seen

WESTERN CAPE.—3320 (Montagu): Matjiesfontein, Memorial Siding, among monuments, (–AB), 1 September 2006, J.C. McMaster s.n. (NBG, photo.), 1 November 2006 (fruit), Manning 3171 (NBG); Komsberg Pass, approximately halfway up pass, (–DB), 22 September 2007, V.R. Clark & C. Kelly 102 (GRA, NBG). 3322 (Oudtshoorn): Prince Albert, hill ENE of village on road to Platberg, (–AA), 31 August 2006, J.P. Roux s.n. (NBG, photo.).

***Gladiolus reginae* Goldblatt & J.C.Manning, sp. nov.** (section *Ophiolyza*)

Plantae 0.4–1.5 m altae, cormo subgloboso $\pm$ 20 mm diam., tunics papyraceis vel aetate aliquantum fibrosis, foliis 8 vel 9 inferioribus 6 vel 7 basalibus grandioribus laminis anguste ensiformibus (3–)5–10 mm latis, caule simpliciter vel 1-ramoso, spica erecta 7- ad 16-flora disticha floribus suboppositis vel oppositis, bracteis molli-bus pallide viridibus siccentibus pallide stramineis post anthesin bractea, externa (20–)22–32 mm longa interna ad apicem minute furcata marginibus connatis in dimidio inferiore, floribus pallide carneis, tepalis inferioribus tribus lateraliter atrorubro-suffusis in tertia parte basali, in

dimidio basali striatis, inodoris, tubo perianthii obliquiter infundibuliformi 33–35 mm longo, tepalis inaequalibus superioribus tribus grandioribus ad basem erectis recurvatis distaliter lanceolato-attenuatis marginibus leviter undulatis, tepalo dorsali 33 $\times$ 11–12 mm, superioribus lateralibus 32–34 $\times$ 10–12 mm, inferioribus tribus per 1 mm connatis 29–30 $\times$ 9–10 mm, filamentis 17 mm longis ex tubo 7 mm exsertis, antheris 8–9 mm longis purpureis, stylo arcuato ramis 4 mm longis.

TYPE.—Mpumalanga, 2430 (Pilgrim's Rest): Kennedy's Vale, Two Rivers Mine, hills west of bridge over Klein Dwarsrivier, (–CC), 26 March 2008, Manning & Valente 3156 (NBG, holo.; K, MO, NBG, PRE, iso.).

Plants 0.4–1.5 m. Corm subglobose, $\pm$ 20 mm diam.; outer tunics papery, becoming irregularly broken and somewhat fibrous with age. Stem erect or inclined outward above basal leaves, unbranched or occasionally with a branch from axil of uppermost stem leaf, 2–3 mm diam. below spike. Cataphylls brownish above ground. Leaves 8 or 9, lower 6 or 7 basal and largest, reaching to base of spike or above; blades narrowly sword-shaped, (3–)5–10 mm wide, relatively soft-textured with midrib raised but other veins and margins not thickened, slightly twisted in distal half, remaining 2 or 3 leaves cauline and smaller, uppermost largely or entirely sheathing, margins open to base. Spike erect, 7–16-flowered, flowers in two ranks, subopposite and 60–90° apart, or opposite; bracts soft-textured, pale green becoming pale straw-coloured and dry shortly after anthesis, outer (20–)22–32 mm long, inner slightly shorter or $\pm$ as long, minutely forked apically, margins fused in basal half and thus tubular below. Flowers pale flesh-pink, tepal sutures and tube flushed deeper salmon, lower three tepals flushed deep red laterally in basal third, basal half streaked with three main and two minor longitudinal lines, upper three tepals flushed deep red at base and filaments deep red in basal third, unscented; perianth tube obliquely funnel-shaped, slightly arched distally, 33–35 mm long, basal cylindrical portion 25–27 mm long; tepals unequal, upper three larger, erect below, recurved in distal half, lanceolate-attenuate, margins slightly undulate, dorsal tepal horizontal in basal half and deeply concave, 33 $\times$ 11–12 mm, upper laterals 32–34 $\times$ 10–12 mm, lower three tepals joined for an additional 1 mm, lower laterals shortest, 28–29 $\times$ 9–10 mm, lower medial 30 $\times$ 9–10 mm. Filaments 17 mm long, exserted 7 mm from tube; anthers 8–9 mm long, purple; pollen cream-coloured. Ovary ovoid, $\pm$ 6 mm long; style arching beneath dorsal tepal, dividing at or beyond anther tips, branches 4 mm long. Capsule obovoid, 30 $\times$ 12 mm, 3-lobed and retuse apically. Seeds oval to oblong, 8–10 $\times$ 4–6 mm, $\pm$ evenly winged or wing not developed on one side, rich brown, seed body relatively large, $\pm$ 3 mm diam. Flowering time: mid-March to mid-April. Figure 4.

Distribution and ecology: *Gladiolus reginae* is currently known only from two populations along the lower slopes of the Dwarsrivier Mountains (Figure 5), one on the Two Rivers Platinum Mine concession and the second on Steelpoort Park, some 5 km to the west. Plants grow in open woodland, partially shaded by shrubs and trees, and are largely restricted to rocky outcrops, where the corms are wedged in pockets of humus between the



FIGURE 4.—*Gladiolus reginae*, Manning & Valente 3156 (NBG). A, corm and flowering stem; B, inner bract; C, half flower; D, capsule and seeds. Scale bar: 10 mm. Artist: John Manning.

rocks. Geologically the substrate has been identified as the igneous rock gabbro-norite (G. Deall pers. comm.), which contains slightly higher concentrations of heavy metals than granite, thus weathering into heavy metal-enriched soils (Van Wyk & Smith 2001). *G. reginae* may thus be considered another of the several edaphic endemic species of *Gladiolus* that have been identified in Iridaceae (Goldblatt & Manning 1996, 1998).

The Dwarsrivier is a tributary of the Steelpoort River, which bisects the Sekhukhuneland Centre of Floristic Endemism identified by Van Wyk & Smith (2001). This mountainous region is relatively poorly known botanically but its rocks hold large reserves of chrome and platinum-group metals, and the area supports a rich flora of local edaphic endemics. *Gladiolus reginae* is one of two

Gladiolus species endemic to the Sekhukhuneland Centre. The first to be described, *G. sekukuniensis* P.J.D. Winter, is restricted to alkaline calcretes (Manning *et al.* 1999). Although over 100 species of plants are estimated to be endemic or near-endemic to the Sekhukhuneland Centre (Van Wyk & Smith 2001), the endemic Iridaceae thus far known include just these two species of *Gladiolus*. As far as is known, *Gladiolus* is the only genus of Iridaceae in which species have evolved that are tolerant of heavy metals (Goldblatt & Manning 1996, 1998).

The long-tubed, unscented, pale pink flowers of *Gladiolus reginae* are evidently adapted to pollination by long-proboscid flies, and its co-occurrence with the labiate shrub *Orthosiphon tubiformis*, which is pollinated by *Stenobasipteron wiedmannii* (Nemestrinidae) (Goldblatt

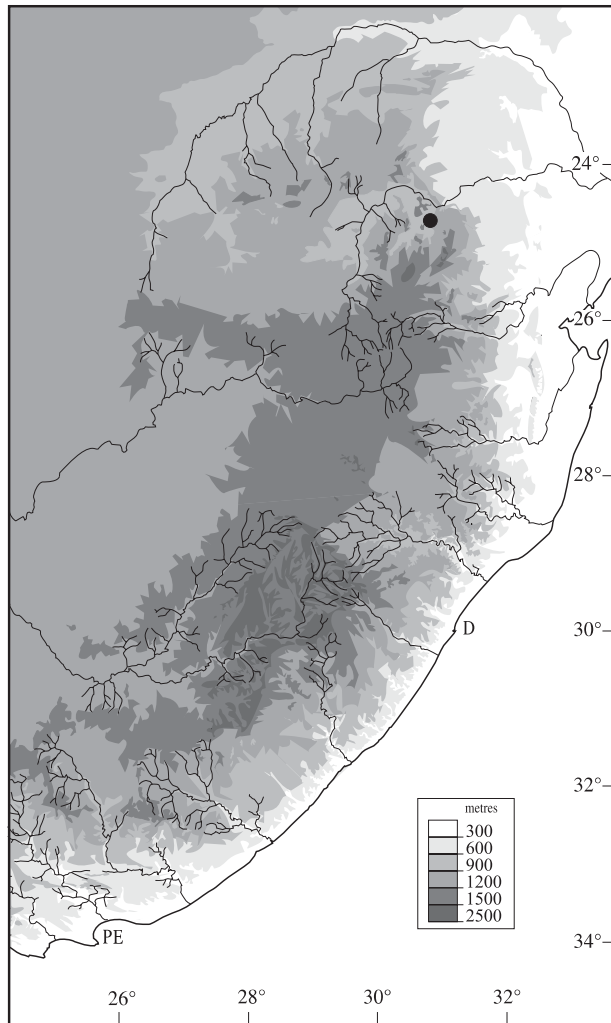


FIGURE 5.—Known distribution of *Gladiolus reginae*, ●.

& Manning 1999) makes it all but certain that *G. reginae* is a member of this pollination guild. Intriguingly, the species exudes minute droplets of dilute photosynthate from the tips of the inner and outer bracts. These attract numerous ants, which crawl over the inflorescence axis among the flowers. We noted a similar strategy in *G. pole-evansii* J.Verd. (Goldblatt & Manning 1998) and speculated that ants may play a defensive role in deterring predators. This phenomenon had not been noted in any other species of *Gladiolus*.

The species was brought to our attention by Graham Deall, who encountered a population near Steelpoort dur-

ing a botanical survey of the area in February 2006. In the same season a second population was photographed in the nearby Twin Rivers Platinum Mine concession by geologist Louise Fouche. A visit to the Steelpoort locality in February 2007 after a very dry summer was unsuccessful and the corms had evidently failed to sprout. Good flowering plants were, however, found on a second visit to the Twin Rivers Platinum Mine site in March 2008, following good summer rains. Although plants appear to be locally common where they occur, the extent of the species distribution is evidently very limited, making it vulnerable to increased transformation of the habitat.

Diagnosis and relationships: despite the lack of pubescence on the stems or leaves, numerous features point to a relationship with members of series *Scabridus*. These include the tall stature of the plants and their narrow, relatively soft-textured leaves without visibly thickened margins, papery outer corm tunics, ± erect spike with 2-ranked, moderately sized, pink flowers, thin-textured, pale bracts, and large, obovoid capsules. Its habitat, in hot, dry savanna, is also consistent with this relationship. Within the series, *Gladiolus reginae* is florally most similar to *G. scabridus* M.P.de Vos from northern KwaZulu-Natal but the glabrous stem and leaves, and the pale salmon or flesh-pink flowers with a deep red centre, including the base of the filaments, points to a closer relationship with *G. pavonia* Goldblatt & J.C.Manning from northeastern Mpumalanga. *G. reginae* differs from *G. pavonia* in lacking the characteristic stolons of the latter species, in its longer floral tube, 33–35 mm vs. ± 16 mm, and in its attenuate rather than acute tepals.

In general appearance, particularly the long-tubed pink flowers with tubular inner bracts, *Gladiolus reginae* resembles *G. dolomiticus* Oberm., another savanna species from northern South Africa. This dolomite endemic, however, is covered with a velvety pubescence on leaves and stem, the leaf blades are distinctly fibrotic, have thickened margins, the flowers have a shorter tube, 18–27 mm long, and the lower tepals are marked with a median pale blotch rather than with red streaks.

Etymology: Latin *reginae*, queen, after the legendary Queen of Sheba (Saba), who controlled rich gold mines in eastern Africa, in a reference to both the type locality of the species on the site of a platinum mine and to the beauty of its flowers.

Other material seen

MPUMALANGA.—2430 (Pilgrim's Rest): Steelpoort Park, (–CC), March 2006 (photo.), April 2006 (fruit), *G. Deall* s.n. (NBG).

IDENTIFICATION KEYS

The following replacement couplets are provided for insertion in the relevant keys to the species published in *Gladiolus in southern Africa* (Goldblatt & Manning 1998).

Key to section *Blandus* (page 52)

13. Perianth tube longer than the dorsal sepal, (30–)40–100 mm long
14. Tepals attenuate and strongly undulate; lower tepals slightly shorter than the upper *G. undulatus*
- 14'. Tepals obtuse to acute, not attenuate and weakly undulate; lower tepals usually about two-thirds as long as the upper
15. Leaves four or five; flowers cream to yellowish with prominent spear-shaped markings in red on the lower tepals; flowering October to November; West coast mountains and flats *G. angustus*
- 15'. Leaves three to seven; flowers salmon with red linear markings on the lower tepals; flowering February to April; southern Cape and Little Karoo

- 15a. Leaves three, the blades 6–8 mm wide; perianth tube 50–70 mm long; flowering March and April, southern foothills of the Langeberg *G. bilineatus*
 15a'. Leaves six or seven, the blades 1.5–6.5 mm wide; perianth tube 30–55 mm long; flowering February, Little Karoo mountains. *G. dolichosiphon*
 13'. Perianth tube shorter than to $\pm$ as long as the dorsal tepal, (15–)20–50 mm long

Key to section *Hebea* (page 55)

- 29'. Perianth tube 9–15 mm long; dorsal tepal 16–33 mm long
 29a. Flowers bright yellow; lower lateral tepals with lower half of blade involute-tubular and auriculate *G. karooicus*
 29a'. Flowers whitish to dull grey, purple or brownish yellow; lower lateral tepals with lower half of blade canaliculated and clawed but not auriculate *G. permeabilis*

Key to sections *Densiflorus* and *Ophiolyza* (page 50)

- 60'. Leaves narrow and usually exceeding the spikes, in a lax fan usually arising some distance above the ground; leaf blades always with a prominent midrib and sometimes secondary veins also developed
 60a. Plants glabrous; perianth tube 33–35 mm long; lower tepals streaked with red and base of filaments flushed dull red *G. reginae*
 60a'. Plants glabrous or pubescent; perianth tube 10–27 mm long; lower tepals not streaked and filaments concolorous 7

CLASSIFICATION

The discovery of *Gladiolus reginae*, a member of series *Scabridus* (see above), highlights several morphological inconsistencies in the current placement of the series in section *Densiflorus* Goldblatt & J.C.Manning. These are examined in detail here.

The current classification of *Gladiolus* in southern Africa recognizes seven sections, diagnosed principally by the shape, number and insertion of the leaves on the stem, the shape and number of the flowers, and the size of the capsules (Goldblatt & Manning 1998). Sections *Densiflorus* and *Ophiolyza* (Klatt) Goldblatt & J.C.Manning are characterized by the possession of several basally inserted, lanceolate leaves arranged in a fan, and flowers without distinct spade- or lozenge-shaped markings on the lower tepals. Both are predominantly or entirely restricted to the summer rainfall region. Section *Densiflorus* is recognized by its many-flowered, subsecund spike and small capsules, less than 10 mm long, and section *Ophiolyza* by its generally large stature and especially by flowers with sharply recurved lower tepals.

There is little doubt that *Gladiolus reginae* is correctly placed in series *Scabridus*, despite the lack of the pubescence on leaves and/or stem that characterizes many members of the series. The large stature of the plants, their slender, soft-textured leaves without thickened margins, and the 2-ranked spike of moderately large, pink flowers with the lower tepals marked with red longitudinal lines are all characteristic of the series. Series *Scabridus* is currently included in section *Densiflorus* but its placement at the end of the section and just before section *Ophiolyza* indicates its somewhat intermediate character.

The possibility that the series is incorrectly placed in section *Densiflorus* is highlighted by the observation that *Gladiolus reginae* shares several highly distinctive features with *G. pole-evansii*, a member of section *Ophiolyza*. The most unusual of these is the fusion of the margins of the inner bracts in the basal portion such that they are tubular below. This characteristic was identified as diagnostic of series *Oppositiflorus* by Goldblatt & Manning (1989). Its occurrence in *G. reginae* must thus be interpreted either as a homoplasy, or as evidence for a closer alliance between the species (and by inference

the entire section *Scabridus*) and series *Oppositiflorus*. The shared occurrence of other unusual features in *G. reginae* and *G. pole-evansii*, however, makes the latter interpretation more likely. These include the exudation of droplets from the tips of the bracts and bracteoles (a character unknown elsewhere in the genus), the subopposite or opposite arrangement of the flowers in the spike (a second diagnostic characteristic of series *Oppositiflorus* and found also among several other members of series *Scabridus* but anomalous in section *Densiflorus*), the recurving lower tepals (diagnostic of section *Ophiolyza*) and the large, obovoid capsules (characteristic of most members of series *Scabridus* and anomalous in section *Densiflorus*). Coupled with this is the shared development of velvety pubescence in several members of both series *Scabridus* and *Oppositiflorus* and its otherwise total absence in section *Densiflorus*.

All the evidence thus indicates that series *Scabridus* is misplaced in section *Densiflorus* and is actually closely allied to series *Oppositiflorus* of section *Ophiolyza*. We accordingly move the series to that section. The exact relationship between series *Scabridus* and series *Oppositiflorus* is less easily determined, however, and we retain the two as separate pending further study. Until then it is least disruptive to merely transfer series *Scabridus* from the end of section *Densiflorus* to the beginning of section *Ophiolyza*, a move that will not require rearrangement of the sequence of species in the current classification (Table 2).

TABLE 2.—Summary of revised classification of *Gladiolus* in southern Africa

<i>Gladiolus</i> L.
Section <i>Densiflorus</i> Goldblatt & J.C.Manning [series not listed]
Section <i>Ophiolyza</i> (Klatt) Goldblatt & J.C.Manning
Series <i>Scabridus</i>
Series <i>Oppositiflorus</i>
Series <i>Ecklonii</i>
Series <i>Ophiolyza</i>
Section <i>Blandus</i> (Baker) Goldblatt [series not listed]
Section <i>Linearifolius</i> (M.P.de Vos) Goldblatt & J.C.Manning [series not listed]
Section <i>Heterocolon</i> O.Kuntze [series not listed]
Section <i>Hebea</i> (Pers.) Benth. & Hook. [series not listed]
Section <i>Homoglossum</i> (Salisb.) Goldblatt & J.C.Manning [series not listed]

NEW NAME

***Gladiolus sulcatus* Goldblatt**, nom. nov., pro *G. sulcatus* Goldblatt, *Gladiolus* in tropical Africa: 113 (1996), nom. illeg. non *G. sulcatus* Lam.: 119 (1791) [= *Babiana hirsuta* (Lam.) Goldblatt & J.C.Manning].

The name *Gladiolus sulcatus* Goldblatt (1996) is a later homonym for *G. sulcatus* Lam. (March 1791), now *Babiana hirsuta* (Lam.) Goldblatt & J.C.Manning (= *Babiana thunbergii* Ker Gawl.) (Goldblatt & Manning 2006). We rename the species *G. sulcatus*, thus preserving the reference in the specific epithet to the finely ribbed leaves of this rare species of central Tanzania. Although *G. sulcatus* Lam. is a superfluous name for *Antholyza hirsutus* Lam., it is nevertheless valid (McNeill *et al.* 2006 Art. 52.3). Possibly Lamarck (1791) provided the new epithet in *Gladiolus* because he was aware of the impending publication of *G. hirsutus* Jacq., dated imprecisely as 'late' 1791.

RANGE EXTENSION

Gladiolus rubellus Goldblatt, a member of section *Heterocolon*, is readily recognized by its small, scarlet flowers with bright yellow markings on the lower lateral tepals, hooded dorsal tepal, and linear leaves with thickened margins and midrib, the margins raised at right angles to the blade (Goldblatt 1993; Goldblatt & Manning 1998). It is currently known only from a small region of southeastern Botswana, between the towns of Lobatse and Molepolole. Plants grow in stony ground in dry savanna and flower in late summer and autumn, between January and March.

On a recent field trip to northern Namibia by staff of the South African National Biodiversity Institute, a species of *Gladiolus* was photographed in the Baynes Mountains in the northwest of the country that represents a species not before recorded for the country. It is evidently close to *G. rubellus*, although the flowers may differ slightly in the relative proportions of the lower tepals, possibly less intense red colouring of the perianth, and leaf margins that are thickened rather than raised at right angles to the blade surface. It is difficult to assess these characters more accurately from a single photograph but there is no doubt as to the importance of this record as just three species of *Gladiolus* are currently known from the summer rainfall part of Namibia, *G. dalenii* van Geel, *G. permeabilis* subsp. *edulis* (Burch. ex Ker Gawl.) Oberm. and *G. saccatus* (Klatt) Goldblatt & M.P.de Vos, all of them widespread in southern Africa. Pending the collection of additional material, we include the Baynes Mountain population in *G. rubellus*, thereby extending the range of the species some 1 300 km to the northwest and rendering it no longer endemic to Botswana.

Material examined

NAMIBIA.—1712 (Posto Velho): Cunene Region, Baynes Mountains, Omavanda Mountains, open savanna on gentle SE slope, (–BB), 25–30 April 2008, G. Nicolson s.n. (NBG, photo.).

ACKNOWLEDGEMENTS

Support for this study from Elizabeth Parker, and by grant 7799-05 from the National Geographic Society, are gratefully acknowledged. Collecting permits were provided by the Nature Conservation authorities of Northern Cape and Western Cape, South Africa. We thank Lendon Porter and Elizabeth Parker for their assistance and companionship in the field; Graham Deall for collecting fruiting material of *Gladiolus reginae* and for guiding us to the species; AnneLise and Jan Vlok for collecting material of *Gladiolus dolichosiphon*; and Greg Nicolson for alerting us to the existence of *G. rubellus* in Namibia.

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A revision of Fumariaceae (Fumarioideae) in southern Africa, including naturalized taxa

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Keywords: *Cysticapnos* Mill., *Discocapnos* Cham. & Schltdl., *Fumaria* L., Fumariaceae, southern Africa, taxonomy, *Trigonocapnos* Schltr.

ABSTRACT

The native and naturalized species of Fumariaceae in southern Africa are reviewed, and keys and full descriptions are provided. All relevant regional synonyms are given and the indigenous species are illustrated. Three native genera with four species are recognized. The previously taxonomically unplaced genus *Cysticapnos* Mill. (3 spp.) is included with two other monotypic native South African genera, *Discocapnos* Cham. & Schltdl. and *Trigonocapnos* Schltr., in an enlarged circumscription of subtribe Discocapninae, which is morphologically defined by tendrilliferous leaves and mostly sessile racemes with the lowermost flower basal. Two subspecies are recognized in *Cysticapnos vesicaria* (E.Mey. ex Bernh.) Lidén, subsp. *vesicaria* with fewer, smaller flowers and subsp. ***namaquensis*** J.C.Manning & Goldblatt for plants from Namaqualand with more numerous, often larger flowers. *C. parviflora* Lidén appears to be nothing more than a dwarf-fruited form of *C. vesicaria*, in which heterocarpy has long been known. *C. pruinosa* (E.Mey. ex Bernh.) Lidén is recorded for the first time to be a short-lived perennial and not an annual, thus unique in the tribe Fumarieae. *Discocapnos mundii* var. ***dregei*** Harv. from the southern Cape is treated as subsp. ***dregei*** (Harv.) J.C.Manning & Goldblatt on account of its slightly smaller fruits and significant geographical disjunction from subsp. *mundii*. Three introduced species are included, *Fumaria capreolata* L., *F. muralis* Sond. ex W.D.Koch subsp. *muralis* and *F. parviflora* Lam. var. *parviflora*, although only the last two appear to be truly naturalized.

INTRODUCTION

Fumariaceae are a well-circumscribed family, sister to a monophyletic Papaveraceae *sensu stricto* (APG 2003). Although included in a broader circumscription of Papaveraceae by some authors, e.g. Bremer *et al.* (2003), the two groups represent reciprocally monophyletic clades that are optionally retained as separate families (APG 2003). We adopt the latter option, following Lidén (1993) as the most recent complete classification of Fumariaceae. Treating Fumariaceae in Papaveraceae as subfamily Fumarioideae has nomenclatural implications on the rank of lower-order taxa that have yet to be fully implemented.

Fumariaceae are readily distinguished from Papaveraceae by the colourless or yellow, watery or translucent (not milky) exudate, strongly zygomorphic or bilaterally symmetric flowers with small sepals, and petals that are not crumpled in bud. In addition, one or both of the outer petals are spurred basally, the stamens are usually connate into two bundles, and the bicarpellate, syncarpous ovary ripens into a capsule or nut (Bremer *et al.* 2003; Lidén 1993).

Fumariaceae are primarily north temperate, comprising 17 genera and $\pm$ 530 species. The family is taxonomically relatively well understood (Lidén 1993), and comprises the two subfamilies Fumarioideae (DC.) Endl. and Hypecoideae (Dum.) Prantl

& Kündig, the latter consisting of the single genus *Hypecoum* L. from the Mediterranean and Asia. Subfamily Fumarioideae includes the tribe Corydaleae Rchb., characterized by many-seeded capsules containing seeds with a conspicuous elaiosome, and the tribe Fumarieae, mostly with nuts or few-seeded capsules, usually a caducous style, and seeds lacking an elaiosome. The tribe Fumarieae is in turn divided into the three subtribes Sarcocapninae Lidén, Fumariinae, and Discocapninae Lidén.

The family is poorly represented in sub-Saharan Africa with just two species known from tropical Africa (Lucas 1962), *Fumaria abyssinica* Hamm. and *Corydalis milderbraedii* Fedde. Both are widely distributed from Ethiopia to Kenya and Tanzania, and represent large genera that are primarily northern hemisphere in distribution. This contrasts sharply with the situation in southern Africa, which is home to five species in three genera, all endemic to the sub-region. Two of these genera, *Discocapnos* Cham. & Schltdl. and *Trigonocapnos* Schltr., are monotypic and together comprise subtribe Discocapninae Lidén but the third genus *Cysticapnos* Miller (3 spp.) is not currently placed at tribal level (Lidén 1986, 1993). The subtribe Discocapninae is characterized by tendrilliferous leaves and single-seeded, pubescent achenes. *Cysticapnos* has similar tendrilliferous leaves but a many-seeded, dehiscent, capsular fruit. DNA studies (Forest & Manning in prep.) indicate that the three southern African genera, *Cysticapnos*, *Discocapnos* and *Trigonocapnos* constitute a monophyletic lineage within Fumarieae, and all three genera are thus most appropriately accommodated in an enlarged Discocapninae. The subtribe is defined morphologically by its tendrilliferous leaves, found elsewhere in the family only in the Mediterranean genus *Ceratocapnos* Dur. (tribe Fumarieae subtribe Sarcocapninae) and in

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MS. received: 2008-08-06.

Dactylicapnos Wall. (tribe Corydaleae Rchb.) from the Himalayas. Several of the species also have sessile racemes (the lowermost flower arising at the base of the peduncle), whereas other genera of Fumariaceae typically have distinctly pedunculate racemes (the lowermost flower inserted well above the base of the peduncle). Anatomy of the seed coat is essentially identical in *Cysticapnos*, *Discocapnos* and *Trigonocapnos* (Fukuhara & Lidén 1995a) and also in several other genera of Fumariaceae and Corydaleae, thus offering no additional synapomorphies for the subtribe. Of potentially greater interest is the observation that *Discocapnos* and *Trigonocapnos* share an unusual vasculature of the fruit wall in which the funicular supply is ultimately derived from the ventral and dorsal bundles rather than from the lateral bundles as in other fumarioids (Fukuhara 1995; Fukuhara & Lidén 1995b). Unfortunately the pericarp vasculature of *Cysticapnos* has not been studied and it is therefore not known which pattern it follows.

The molecular analysis (Forest & Manning in prep.) retrieves *Discocapnos* as sister to *Trigonocapnos* plus a monophyletic *Cysticapnos*, with the entire clade sister to *Fumaria* L. This relationship supports the interpretation that the nutlet is plesiomorphic for the subtribe Discocapninae and that the capsules of *Cysticapnos* represent an autapomorphy for the genus. This topology offers two logical alternatives for circumscribing genera in the subtribe Discocapninae. The first retains three separate genera as circumscribed by Lidén (1986, 1993), whereas the second includes *Discocapnos* and *Trigonocapnos* within an enlarged *Cysticapnos*. The latter treatment is not consistent with the current circumscription of genera in the family (Lidén 1993), in which fruit type is extensively used as the basis for separating related genera, resulting in constellations of oligotypic genera clustered around the two large genera *Corydalis* DC. and *Fumaria*. The merits of this approach may be debated but at this stage it is unjustifiable to treat the southern African genera in a radically different way in the face of the molecular evidence that they are indeed monophyletic as currently construed. The capsular fruits of *Cysticapnos* represent a significant evolutionary innovation that in the current classification justifies its retention as a separate genus. Any changes to generic circumscriptions in the tribe Discocapninae are best done in the context of a reappraisal of the entire family. The southern African clade is adequately identified as the subtribe Discocapninae for purposes of biogeographic or phylogenetic investigation.

capninae for purposes of biogeographic or phylogenetic investigation.

The first southern African species of Fumariaceae to be described were placed either in the genus *Corydalis* (capsular-fruited species) or *Fumaria* (those with nutlets). The varied and distinctive fruits of several of the southern African taxa, however, soon led to their taxonomic separation into distinct genera, beginning with the genus *Cysticapnos* (Miller 1754), erected for the bladder-fruited species that was until then known as *Corydalis vesicaria* L. The genus *Phacocapnos* Bernh. was later described (Bernhardi 1838) for the remaining capsular-fruited species with compressed fruits but is now included within *Cysticapnos* (Lidén 1986). The two nutlet-fruited species remain respectively in the monotypic genera *Discocapnos* (Chamisso & Schlechtendel 1826) and *Trigonocapnos* (Schlechter 1899).

The southern African Fumariaceae were first reviewed by Harvey (1894) for *Flora capensis* and later more thoroughly by Hutchinson (1921) as part of his treatise on the biogeography of the family. The most recent, and only modern revision of the southern African species, is the worldwide study of the family by Lidén (1986), in which the current generic concepts and classification were established, and the application of the names of the species was fixed. A milestone in the study of the family, this treatment is nomenclaturally incomplete and is also based on examination of very limited material of the southern African taxa, essentially the types. With more extensive material available, it is evident that two of the species recognized there, viz. *Cysticapnos grandiflora* sensu Lidén and *C. parviflora* Lidén, cannot be upheld. In addition, the patterns of geographical variation shown in both *C. vesicaria* and *Discocapnos mundii*, support the recognition of subspecies in each. We provide here a complete, illustrated account of the native species of southern African Fumariaceae, based on extensive field and herbarium study. Three introduced species of *Fumaria* that have become $\pm$ naturalized are also included, following the taxonomy of Lidén (1986).

MATERIALS AND METHODS

This study is based on an examination of living plants in the field and of specimens in the following herbaria: BOL, K, MO, NBG, NU, PRE, TCD (acronyms as in Holmgren *et al.* 1990). The abbreviation of authors' names follows Brummitt & Powell (1992).

Key to genera of Fumariaceae in southern Africa

- 1a Leaves not tendrilliferous; racemes pedunculate; style twice or more as long as ovary, caducous; fruiting pedicels usually suberect, thickened; fruit a subglobose nutlet with woody endocarp subtribe Fumariinae: *Fumaria* (introduced species)
- 1b Terminal leaflets of some or all leaves developed into tendrils; racemes pedunculate or sessile (lowermost flower basal); style $\pm$ as long as ovary or shorter, usually persistent; fruiting pedicels recurved, not thickened; fruit a capsule or achene, without woody endocarp subtribe Discocapninae:
 - 2a Fruit a several-seeded capsule; spur on upper petal $\pm$ as long as wide or shorter; style less than half as long as ovary, persistent 3. *Cysticapnos*
 - 2b Fruit a 1-seeded, pubescent or scabridulous achene; spur on upper petal $\pm$ twice as long as wide; style $\pm$ as long as ovary, persistent or caducous:
 - 3a Flowers and fruit with pedicels $\pm$ 1.5 mm long; achene disciform, sparsely puberulous; style persistent 1. *Discocapnos*
 - 3b Flowers and fruit with pedicels 3–4 mm long; achene obovate-trigonal, densely scabridulous; style caducous 2. *Trigonocapnos*

I. Subtribe **Discocapninae** Lidén, Opera Botanica 88: 104 (1986), emend. J.C.Manning & Goldblatt. Type genus: *Discocapnos* Cham. & Schltdl.

Scandent annuals or rarely perennial (one species only) with bipinnate, tendrilliferous leaves. *Racemes* pedunculate or sessile (lowermost flower basal). *Flowers* pink with purple tip, upper petal spurred, inner petals apically keeled or winged. *Style* usually persistent (rarely deciduous); stigma with two papillae. *Fruit* either a many-seeded capsule or a one-seeded achene, without a woody endocarp.

Three genera: *Cysticapnos*, *Discocapnos* and *Trigonocapnos*. Southern Africa.

1. **Discocapnos** Cham. & Schltdl., Linnaea 1: 569 (1826); Harv.: 18 (1894); Hutch.: 114 (1921); Lidén: 104 (1986), 316 (1993). *Fumaria* sect. *Discocapnos* (Cham. & Schltdl.) Prantl in Prantl & Kündig: 145 (1891). Type species: *D. mundii* Cham. & Schltdl.

Brittle, semi-succulent, glabrous, climbing annual; stems quadrate, with obscure unicellular papillae along angles; sap watery, yellow. *Leaves* alternate, bipinnately compound, primary divisions alternate, ultimate leaflets obovate and 3-partite; terminal leaflets of all or only upper leaves transformed into tendrils. *Inflorescence* pedunculate, terminal but leaf-opposed through rapid growth of axillary bud, racemose; bracts scale-like, petaloid, irregularly toothed. *Flowers* zygomorphic, bilabiate, pink, unscented. *Sepals* 2, lateral, much shorter than petals, scale-like, petaloid, irregularly toothed. *Petals* 4 in 2 series, outer petals larger, naviculate-spathulate, laterally winged apically, upper spurred at base, inner petals apically connate, clawed, limb inflated with dorsal crest, claw basally adnate to upper petal. *Stamens* 6, diadelphous in abaxial and adaxial bundles of 3; filaments of each bundle fused, lanceolate, membranous, clasping ovary, upper filament cluster adnate to margins of dorsal petal basally to form small chamber, with nectary decurrent on dorsal petal into spur. *Ovary* suborbicular, dorsoventrally compressed with peripheral rim, bearing unicellular papillae; ovule solitary, lateral; style short, $\pm$ as long as ovary, flexed upwards apically, persistent; stigma compressed, 2-lobed. *Fruit* pendulous, dorsoventrally compressed, suborbicular with peripheral wing, pubescent, indehiscent and dropping entire, papery. *Seed* solitary, lenticular, glossy black, colliculate, without elaiosome.

One sp., South Africa, southwestern and southern Cape.

1.1. **Discocapnos mundii** Cham. & Schltdl. [as 'mundtii'] in Linnaea 1: 569 (1826); Harv.: 18 (1894); Hutch.: 114 (1921). Lidén: 104 (1986). *Fumaria mundtii* (Cham. & Schltdl.) Prantl & Kündig: 145 (1891). Type: South Africa, Cape of Good Hope, without precise locality, August [without year], *Mund & Maire s.n.* [B-WILLD, holo.].

Climbing annual up to 1 m, with yellow sap. *Leaves* bipinnately compound, rachis flexuose, ultimate segments broadly obovate, 2- or 3-lobed almost to base, lobes elliptical to obovate, terminal segments transformed into tendrils. *Inflorescence* up to 100 mm long in fruit, 8–15-flowered; pedicels erect, apically recurved,

± 1.5 mm long; bracts erect, clasping pedicel, $\pm 1 \times 0.5$ mm, irregularly toothed. *Flowers* pale pink with dark reddish tips. *Sepals* peltate, ovate, $\pm 1.0 \times 1.5$ mm, irregularly toothed. *Petals*: outer petals naviculate-spathulate, $4.5\text{--}5.0 \times 1.0\text{--}1.5$ mm, apically short-winged, wings patent, ± 0.5 mm wide, upper spurred at base, spur $2.5\text{--}3.0$ mm long; inner petals ± 4 mm long, claw ± 1.5 mm long, adnate to upper petal in lower 1 mm, blade inflated, ellipsoid, 2.5×1 mm, with fleshy dorsal crest ± 1 mm wide. *Stamens*: filament bundles lanceolate, $2.5\text{--}3.0 \times 1$ mm, basal nectary decurrent up back of upper petal spur to near apex, vestigial; anthers ± 0.25 mm long, yellow. *Ovary* discus-shaped, 2×2 mm, green, minutely papillate; style maroon, flexed sharply upwards apically, ± 1.5 mm long, persistent. *Fruit* pendent, discus-shaped with peripheral, radially costate wing, (3–)4–5 mm diam., pubescent with unicellular trichomes longest over seed-body, papery, indehiscent and dropping entire, brownish black when mature. *Seed* lenticular, (3–)4–5 mm diam., glossy black, colliculate. *Flowering time*: (August) October–December. Figure 1.

Distribution and ecology: apparently a rare species, with a discontinuous distribution along the cooler, southern foothills of the coastal mountains of the southwestern and southern Cape (Figure 2). The species has been recorded from the Cape Peninsula and adjacent mountains in the southwest, and then some 300 km to the east in the Outeniqua and Tsitsikamma Mountain ranges. *Discocapnos mundii* is restricted to moist, loamy or humic soils on the edge of forest and bush clumps, usually in sheltered valleys or drainage lines, where plants scramble among bushes and grasses. Its distribution tracks the scattered occurrence of afrotemperate forests in the southwestern and southern Cape but it is curious that the species has not been recorded from forest patches along the southern slopes of the intervening Riviersonderend or Langeberg ranges. The plants are, however, inconspicuous and easily overlooked and suitable habitats in these mountain ranges should be investigated in search of additional populations linking the two known areas of occurrence.

Diagnosis and relationships: *Discocapnos mundii* is recognized by its distinctive, discus-shaped samaras containing a solitary seed with a colliculate testa. The seeds of the other southern African species of *Fumariaceae* have scalariform-colliculate surface sculpturing. The one-seeded, indehiscent fruits with pubescent pericarp are shared with *Trigonocapnos lichtensteinii* but the trichomes in *D. mundii*, with their uniquely sculptured cuticular ornamentation (Lidén 1986), are already evident at anthesis rather than developing after fertilization, as in *T. lichtensteinii*, possibly indicating that the pericarp vestiture is independently derived in the two species. Other similarities between the two include the flexuous leaf rachis with the primary divisions of the blade alternate, unlike those of *C. cracca* and *C. vesicaria*, which are often opposite, the strongly spurred dorsal petal, and the relatively rudimentary wings on the lower petal. These characters, however, are also shared with *Fumaria* and are thus evidently ancestral conditions and thus not indicative of a sister-species relationship.

History: the species has an uncomplicated history, presumably on account of its rarity and distinctive fruits.

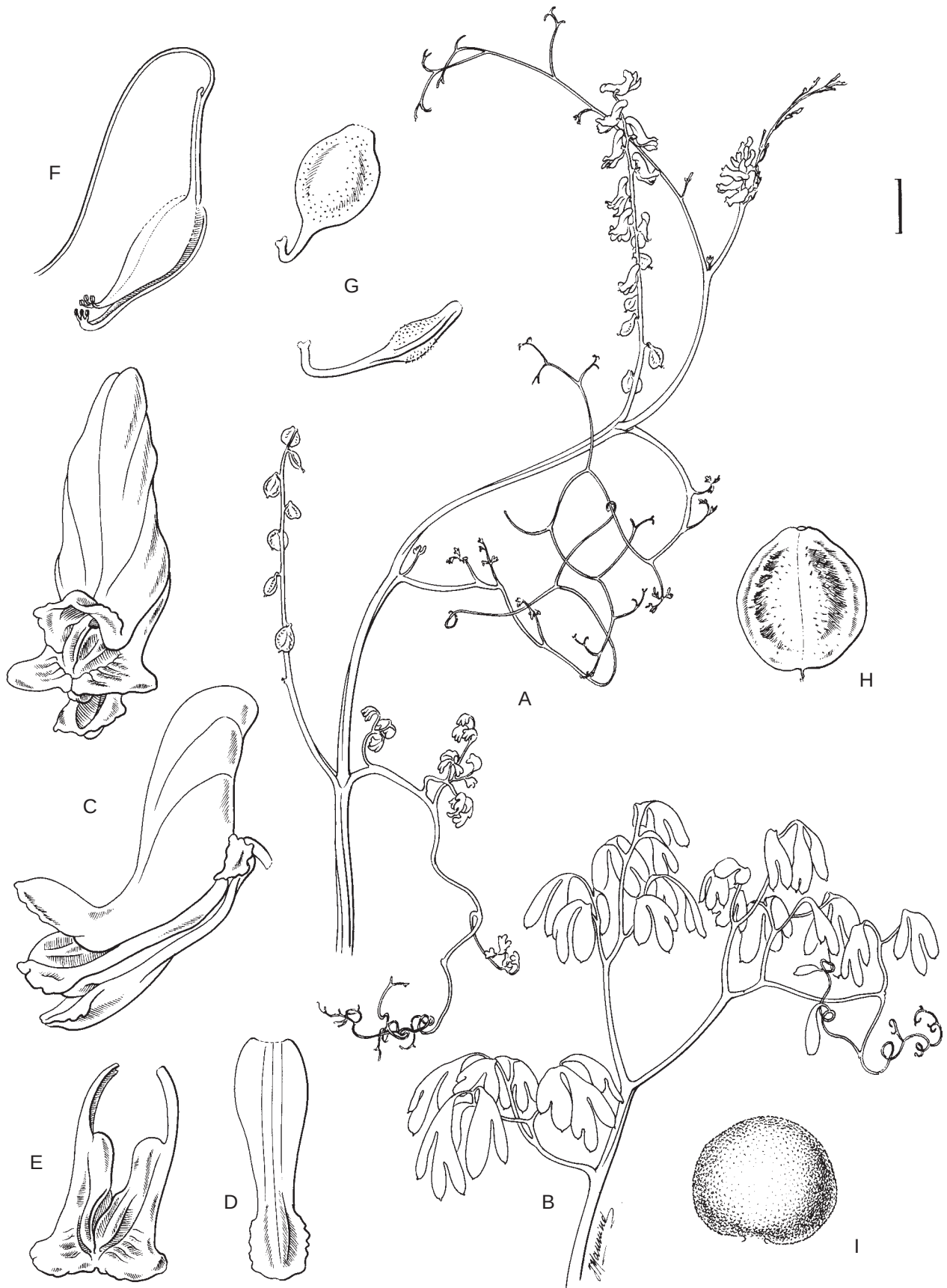


FIGURE 1.—*Dicocapnos mundii* subsp. *mundii*: A, portion of stem; B, lower leaf; C, flower, front and lateral views; D, lower outer petal; E, inner petals; F, androecium and section through spur; G, gynoecium, dorsal and lateral views; H, fruit; I, seed. Scale bar: A, B, 10 mm; C–G, 1 mm; H, 1.6 mm; I, 1.2 mm. Artist: John Manning.

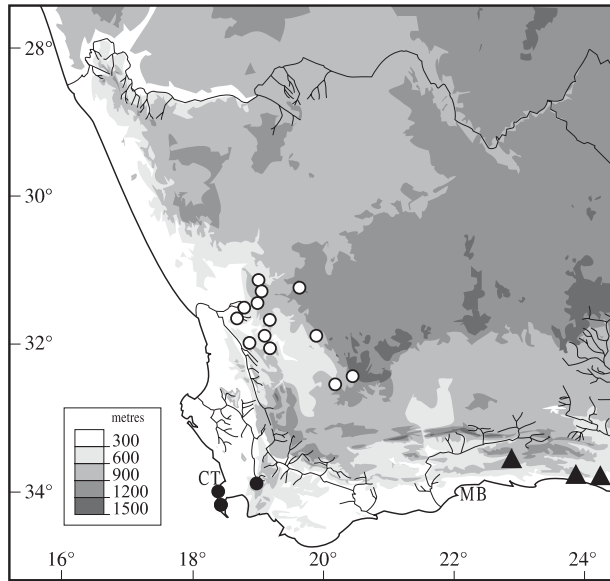


FIGURE 2.—Known distribution of *Discocapnos mundii* subsp. *mundii*, ●; *D. mundii* subsp. *dregei*, ▲; and *Trigonocapnos lichtensteinii*, ○.

It was first collected by the German pharmacist Johannes Mund, who had been despatched to the Cape in 1816 as official plant collector by the Prussian government (Gunn & Codd 1981). His fruiting collection of *Discocapnos mundii* was made in the vicinity of Cape Town, probably soon after his arrival. Mund met Chamisso in Cape Town in 1818 (Gunn & Codd 1981), who subsequently named the species for him (Chamisso & Schlechtendel 1826) in the new genus *Discocapnos* on account of its unusual disc-like fruit. It has been recognized under this name ever since. The original spelling of the epithet as *mundtii* should be treated as an orthographic error and corrected to *mundii* (McNeil *et al.* 2006: Art. 60.7) since his letters to Hooker are signed L. Mund (Gunn & Codd 1981).

Key to subspecies

- 1a Fruits mostly 4–5 mm long subsp. *mundii*
 1b Fruits ± 3 mm long subsp. *dregei*

1.1a. subsp. *mundii*

Fruits (3.5)4–5 mm diam., with peripheral wing 0.8–1.0 mm wide.

Distribution: restricted to the southwestern Cape and mostly recorded from the Cape Peninsula, where it is best known from the lower slopes of Table Mountain between Devil's Peak and Constantiaberg, with additional collections from the northern Hottentots Holland Mountains around Jonkershoek (Figure 2).

1.1b. subsp. *dregei* (Harv.) J.C.Manning & Goldblatt, stat. nov.

D. mundii [as *mundtii*] var. *dregei* Harv. in *Flora capensis* 1: 18 (1894). *D. dregei* (Harv.) Hutch.: 114 (1921). Type: South Africa, [Western Cape], Knysna, Bosch River, between the bush and the river, October 1839, Drège s.n. (TCD, holo.!, K, S, iso.!).

Fumaria scandens E.Mey.: 125, 186 (1844), nom. nud.

Fruits 3.0–3.5 mm diam., with peripheral wing 0.5–0.8 mm wide.

Distribution: known from three collections along the southern foothills of the Outeniqua and Tsitsikamma Mountains, between Knysna and Humansdorp (Figure 2).

Distinguished from the typical subspecies by its slightly smaller fruits, 3.0–3.5 mm diam., with narrower wing less than 1 mm wide.

History: this taxon is based on a collection made near Knysna by the German botanical collector Johann Drège in October 1839. Ernst Meyer, who wrote the botanical accounts of Drège's collections, intended to describe the species as *Fumaria scandens*, and this name appears on the TCD sheet but was never published beyond its appearance in Drège's *Zwei pflanzengeographische Dokumente* (1844). The smaller fruits of these plants compared with those of the typical forms from the Cape Peninsula led Harvey (1894) to distinguish them as the variety *dregei*, which he further defined by its more floriferous racemes. The taxon was subsequently recognized as a distinct species by the British botanist John Hutchinson (1921) in his account of the family. Further collections of the typical form show that there are no differences in floral characters between the two sets of populations. The difference in fruit size did not impress Lidén (1986), who treated them as comprising a single entity, and indeed there are apparently no significant floral or vegetative differences between the two sets of populations. A subsequent collection of var. *dregei* from Clarkson (*Thode s.n.* BOL) confirms that the eastern populations are consistently smaller-fruited but the size difference between the two sets of populations is slight, and a plant from Jonkershoek (*Levy's 8511* BOL) bears occasional fruits of 3.5 mm diam. among the more typical larger fruits of 4 mm diam. The slight but consistent difference in average size of the fruits between the western and eastern populations, combined with the significant disjunction between them, supports taxonomic recognition at some level, and we treat them as subspecies.

2. *Trigonocapnos* Schltr. in *Botanische Jahrbücher* 27: 131 (1899); Hutch.: 113 (1921); Lidén: 105 (1986), 316 (1993). Type species: *T. curvipes* Schltr. [= *T. lichtensteinii* (Cham. & Schltdl.) Lidén].

Brittle, semi-succulent, glabrous, climbing annual; stems quadrate, with obscure unicellular papillae along angles; sap watery, yellow. *Leaves* alternate, bipinnately compound, primary divisions alternate; ultimate leaflets obovate and 3-partite; terminal leaflets of all or only upper leaves transformed into tendrils. *Inflorescence* shortly pedunculate or sessile, terminal but leaf-opposed through rapid growth of axillary bud, racemose; bracts scale-like, petaloid, irregularly toothed. *Flowers* zygomorphic, bilabiate, pink, unscented. *Sepals* 2, lateral, much shorter than petals, scale-like, petaloid, irregularly toothed. *Petals* 4 in 2 series, outer petals larger, naviculate-spathulate, laterally winged apically, upper spurred at base, inner petals apically connate, clawed, limb inflated with dorsal crest, claw basally adnate to upper petal. *Stamens* 6, diadelphous in abaxial and adaxial bundles of 3; filaments of each bundle fused, lanceolate, membranous, clasping ovary, upper filament cluster adnate to margins of dorsal petal basally to form small chamber, with vestigial nectary decurrent on dorsal petal into spur. *Ovary* obovoid with peripheral rim, concave

abaxially, bearing unicellular papillae; ovule solitary, sub-basal; style short, $\pm$ as long as ovary, flexed upwards apically, deciduous; stigma compressed, 2-lobed. *Fruit* pendulous, dorsally crested with lateral rims folded downwards, thus abaxially conduplicate, puberulous, indehiscent and dropping entire, leathery. *Seed* solitary, narrowly obovoid, yellowish brown, scalariform-colliculate, without elaiosome.

One sp., South Africa, northwestern parts of winter rainfall region.

2.1. *Trigonocapnos lichtensteinii* (Cham. & Schltdl.) Lidén in *Opera Botanica* 88: 105 (1986). *Fumaria lichtensteinii* Cham. & Schltdl.: 568 (1826). Type: South Africa, [Western Cape], Cape of Good Hope, without precise locality or date, *Lichtenstein s.n.* (B-WILLD12938, holo.).

T. curvipes Schltr.: 131 (1899); Hutch.: 113 (1921). Type: South Africa, [Western Cape], Clanwilliam, 21 August 1896, R. Schlechter 8585 (BOL, lecto.!, here designated; S, iso.).

F. capreolata $\beta?$ *burchellii* DC: 130 (1824), name without rank. Type: South Africa, Karoo [Roggeveld], 1 August 1811, Burchell 1298 (not located at B, BM, K or P).

F. eckloniana Sond. in Harv.: 18 (1894), nom. nud.

F. micrantha Licht. ms. *Lichtenstein s.n.* (B-WILLD12938).

Climbing annual up to 1 m, with yellow sap. *Leaves* bipinnately compound, rachis flexuous, ultimate segments broadly obovate, 2- or 3-lobed to base, lobes elliptical, terminal segments transformed into tendrils. *Inflorescence* up to 70 mm long in fruit, 20–40-flowered; pedicels suberect, apically recurved, 3–4 mm long; bracts erect, clasping pedicel, 1.0–1.5 $\times$ 0.5 mm, irregularly toothed. *Flowers* pale pink with dark purple tips. *Sepals* peltate, ovate, $\pm$ 0.5 mm long, irregularly toothed. *Petals*: outer petals naviculate-spathulate, 2.5–3.0 $\times$ 0.5–1.0 mm, apically short-winged, wings patent, $\pm$ 0.5 mm wide, upper spurred at base, spur 2.0–2.5 mm long; inner petals $\pm$ 3 mm long, claw $\pm$ 1.5 mm long, adnate to upper petal in lower 1 mm, blade inflated, ellipsoid, 1 $\times$ 0.75 mm, with fleshy dorsal crest $\pm$ 0.75 mm wide. *Stamens*: filament bundles oblong, 1.5–2.0 $\times$ 1 mm, basal nectary decurrent up back of upper petal spur to near apex, vestigial; anthers $\pm$ 0.1 mm long, yellow. *Ovary* obovoid with peripheral rim, concave beneath, 1 $\times$ 0.5 mm, green, colliculate; style translucent, flexed sharply upwards apically, $\pm$ 1 mm long, basally constricted, deciduous. *Fruit* pendent, obovoid-trigonal, dorsally crested with lateral rims folded downwards, thus abaxially conduplicate, 3 mm long, 1.5 mm high and 1.0 mm wide, puberulous, indehiscent and dropping entire, brown when mature, leathery. *Seed* narrowly obovoid, 2 $\times$ 1 mm, yellowish brown, scalariform-colliculate. *Flowering time*: August–September. Figure 3.

Distribution and ecology: *Trigonocapnos lichtensteinii* occurs along the Bokkeveld–Matsikamma Escarpment southwards through the northern Cedarberg to Clanwilliam, and inland from the foot of the Hantamsberg at Calvinia along the Roggeveld Escarpment as far south as the Koedoesberg at the northwestern edge of the Klein Roggeveld (Figure 2). Plants grow in sheltered, seasonally moist situations, along drainage lines or at the base of rocky outcrops in fine-grained clay soils, where they clamber among the surrounding shrubbery.

Diagnosis and relationships: the tricostate, puberulous achenes are diagnostic for the species, as is the narrowly obovoid seed. The style is basally constricted and deciduous, and in this respect *Trigonocapnos lichtensteinii* more closely resembles species of *Fumaria* rather than the indigenous southern Africa taxa of *Fumariaceae*, in which the style is persistent. The curiously shaped fruit is the result of progressive downward curvature of the margins of the ventrally concave, disc-shaped ovary during ripening of the fruit. In its puberulous, single-seeded, indehiscent fruit, *T. lichtensteinii* most resembles *Discocapnos mundii*, but in that species the fruit is disciform and less obviously puberulous, and contains a rounded, lenticular seed. The trichomes on the fruit of *T. lichtensteinii*, unlike those of *D. mundii*, are lacking in cuticular ornamentation (Lidén 1986) and only develop after anthesis, suggesting that pubescence in the two species may have been independently derived. Other similarities between the two species, notably their flexuous leaves with alternate primary segments, and their strongly spurred flowers with rudimentary apical wings on the outer petals, appear to be ancestral and thus not indicative of a sister-species relationship.

History: the species was first collected sometime in the early years of the nineteenth century by Martin Heinrich Lichtenstein, a German physician and naturalist who accompanied the incumbent Governor of the Cape of Good Hope, J.W. Janssens, as family physician on his arrival in Cape Town at the end of 1802 (Gunn & Codd 1981). Over the next three years, Lichtenstein made three journeys into the interior of the country, all of which passed through the Klein Roggeveld, where he almost certainly collected *Trigonocapnos lichtensteinii*. Although Lichtenstein intended to describe his collection under the name *Fumaria micrantha*, this manuscript name remained unpublished and the species was only formally described more than two decades later, when it was named for him by the German botanists Ludolf von Chamisso and Diederich von Schlechtendal (1826).

The next collection of the species was also made during a journey up to the Roggeveld Escarpment, this time by the English explorer William Burchell on 1 August 1811, who noted in his *Travels in the interior of southern Africa* of 1822 (Burchell 1953: 174) that among the 14 specimens collected that day ‘was a Fumitory so exceedingly like an English species, as hardly to be distinguished from it’. This opinion was evidently shared by Alphonse de Candolle (1824), who distinguished Burchell’s plant only as a form of the European *Fumaria capreolata*, basing his identification on the recurved pedicels that characterize the latter species. Although seen by de Candolle in Burchell’s herbarium, we have been unable to locate this specimen but the description of the cirrhose leaves and relatively long, recurved fruiting pedicels (de Candolle 1824: 130) can only apply to *Trigonocapnos lichtensteinii* among the South African taxa and this, combined with the locality, make its identification certain. The species remained poorly known and Harvey (1894: 18) in his account of the family for *Flora capensis*, following the advice of Sonder, included it in the European species *F. muralis*, as yet another of the multiplicity of ‘book species’ of this variable taxon that so aggravated him.

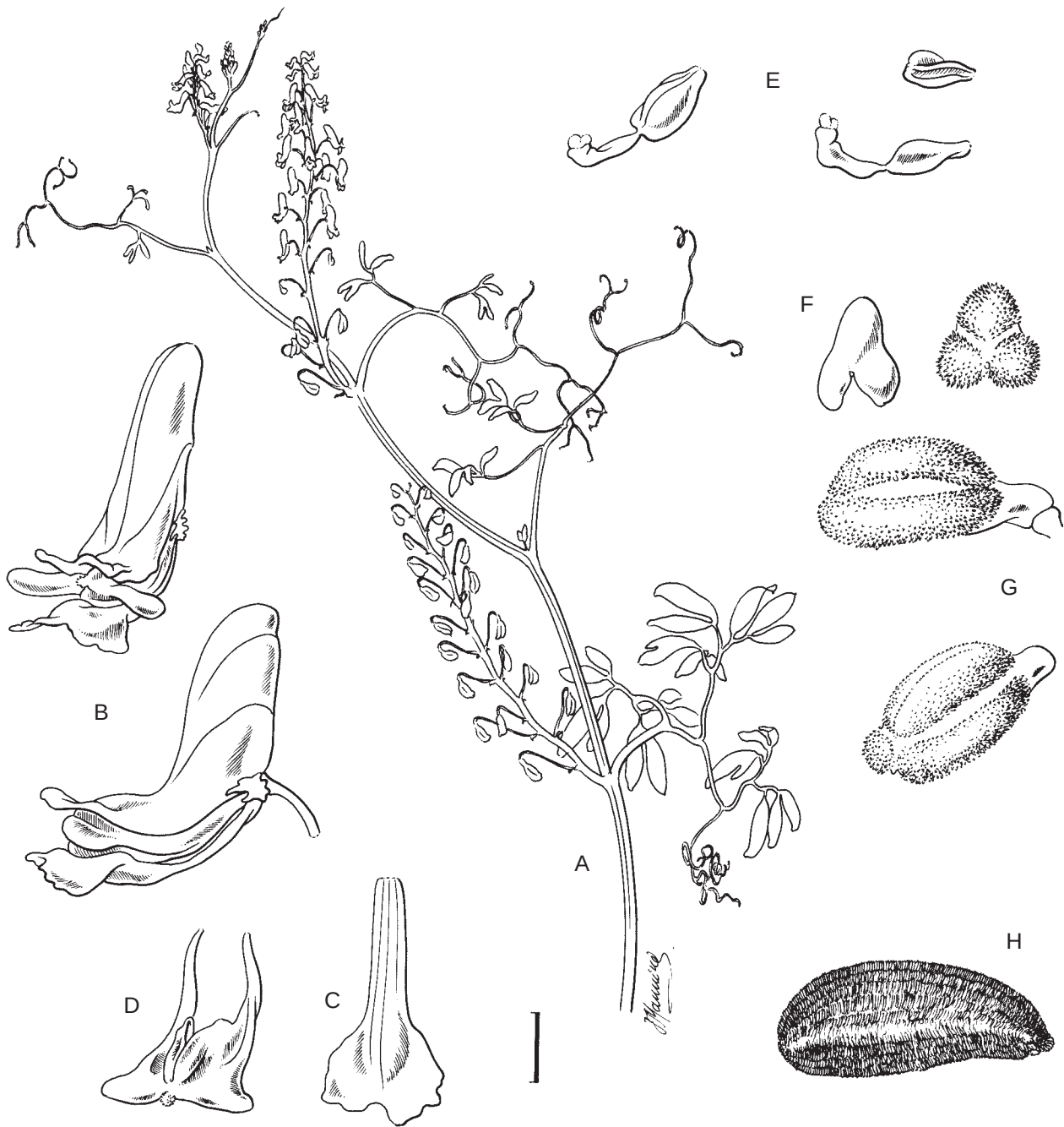


FIGURE 3.—*Trigonocapnos lichtensteinii*: A, portion of stem; B, flower, front and lateral views; C, lower outer petal; D, inner petals; E, gynoecium, dorsal, lateral and partial ventral views, style removed; F, immature fruit, front view; G, mature fruit, front, lateral and three-quarter views; H, seed. Scale bar: A, 10 mm; B–E, G, 1 mm; F, 0.5 mm; H, 0.25 mm. Artist: John Manning.

It is little wonder, therefore, that it was subsequently re-described as a distinct genus by the German botanist Rudolph Schlechter (1899) from a collection that he had made a few years earlier in the Pakhuis Mountains. This is the name under which the species remained known until Lidén (1986) recognized that Chamisso and Schlechtendal's name took priority and accordingly effected its transfer to *Trigonocapnos*. The species is now relatively well known from the Bokkeveld and Pakhuis Mountains but has only been sporadically collected from the Roggeveld and Klein Roggeveld Escarpments.

3. **Cysticapnos** Mill., The gardener's dictionary (1754); Harv.: 16 (1894); Hutch.: 110 (1921); Fedde: 286 (1924); Lidén: 105 (1986), 316 (1993). Type species: *C. vesicaria* (L.) Fedde.

Phacocapnos Bernh.: 664 (1838); Hutch.: 109 (1921). *Corydalis* sect. *Phacocapnos* (Bernh.) Prantl in Prantl & Kündig: 144 (1889); Harv.: 16 (1894). Type species: *P. cracca* (Cham. & Schltld.) Bernh.

Brittle, semi-succulent, glabrous, climbing annuals with slender taproot or rarely (*C. pruinosa*) perennial with fleshy taproot; stems quadrate, with obscure unicellular papillae along angles; sap watery, clear or yellow. Leaves alternate, pinnately or bipinnately compound, primary divisions alternate or opposite; ultimate leaflets elliptical or obovate-cuneate and deeply 3-lobed; terminal leaflets of all or only upper leaves transformed into tendrils. Inflorescence pedunculate or sessile, terminal but leaf-opposed through rapid growth of axillary bud,

racemose; bracts scale-like, petaloid, irregularly toothed. *Flowers* zygomorphic, bilabiate, pink, unscented. *Sepals* 2, lateral, much shorter than petals, scale-like, petaloid, irregularly toothed. *Petals* 4 in 2 series, outer petals larger, naviculate-spathulate, laterally expanded or winged apically, upper saccate or short-spurred at base, inner petals apically connate, clawed, limb inflated with dorsal crest, claw basally adnate to upper petal. *Stamens* 6, diadelphous in abaxial and adaxial bundles of 3; filaments of each bundle fused, lanceolate, membranous, clasping ovary, upper filament cluster adnate to margins of dorsal petal basally to form small chamber, with nectary basal or decurrent on dorsal petal into spur, pulvinate. *Ovary* ovoid, sometimes dorsoventrally compressed, glabrous; ovules several in 2–several series on lateral placentas; style short, straight or geniculate; stigma compressed, 2-lobed. *Fruit* pendulous, capsular, papery, sometimes inflated and bladder-like, circumferentially partially or completely dehiscent. *Seeds* several, lenticular, glossy black, testa obscurely scalariform-colliculate or almost smooth.

Three spp., temperate South Africa, southern Namibia and Lesotho, winter rainfall region and along eastern escarpment to Mpumalanga.

Key to species

- 1a Perennial with fleshy taproot; leaves finely divided, carrot-like; racemes pedunculate, mostly 14–35-flowered; inner petal crests papillate; nectary adnate to lower half of spur; capsules lanceolate-quadrate, transversely flexed 3.2 *C. pruinosa*
- 1b Annuals with slender taproot; leaves not finely divided, *Aquilegia*-like, ultimate segments elliptic; racemes sessile (lowermost flower basal), 1–15(–20)-flowered; inner petal crests smooth; nectary at base of staminal sheath, not adnate to spur; capsules not transversely flexed:
 - 2a Raceme 4–15(–20)-flowered; ± 1 mm long, pedicels shorter than bracts; outer petal wings small, ± 1 mm wide, not extending apically; capsule flattened, lanceolate, 5–12 mm long; style straight; sap yellow 3.1 *C. cracca*
 - 2b Raceme (1)2–7-flowered; pedicels 2–8 mm long, longer than bracts; outer petal wings large, 2–4 mm wide, encircling petal apices; capsule ovoid, usually inflated, 20–25 mm long, rarely dwarfed, 4–10 mm long; style sharply sigmoid at base; sap clear 3.3 *C. vesicaria*

3.1. *Cysticapnos cracca* (Cham. & Schltdl.) Lidén in *Opera Botanica* 88: 108 (1986). *Corydalis cracca* Cham. & Schltdl.: 567 (1826); Harv.: 17 (1894). *Phacocapnos cracca* (Cham. & Schltdl.) Bernh.: 664 (1838); Hutch.: 110 (1921). Type: South Africa, [Western Cape], Cape of Good Hope, without precise locality or date, *Bergius s.n.* (S, holo.).

Phacocapnos dregeanus Bernh.: 664 (1838). Type: South Africa, [Western Cape], Enon, White River, 11 November 1829, *Drège 7586* (MO, holo.!, PRE, iso!).

Corydalis laevigata E.Mey.: 95, 125 (1844), nom. nud.

Climbing annual up to 1 m, with yellow sap. *Leaves* bipinnately compound, ultimate segments broadly obovate, 2- or 3-lobed almost to base, lobes elliptical to obovate, terminal segments transformed into tendrils. *Inflorescence* sessile with lowest flower basal, up to 80 mm long in fruit, 4–15(–20)-flowered; pedicels suberect and slightly curved outwards, ± 1 mm long; bracts recurved, lanceolate, $1.5\text{--}2.0 \times 0.5\text{--}0.75$ mm, irregularly toothed. *Flowers* pale pink with dark reddish tips. *Sepals* ovate, $1.0\text{--}1.5 \times 0.5\text{--}0.75$ mm, irregularly toothed. *Pet-*

als: outer petals naviculate-spathulate, $6.0\text{--}6.5 \times 1.5\text{--}2.0$ mm, apically winged, wings reflexed, ± 1 mm wide, upper saccate at base, sac ± 1 mm deep; inner petals 5–6 mm long, claw ± 3 mm long, adnate to upper petal in lower 1 mm, blade inflated, ellipsoid, $2\text{--}3 \times 1$ mm, with fleshy dorsal crest ± 1 mm wide. *Stamens*: filament bundles lanceolate, $4.0\text{--}4.5 \times 1$ mm, upper bundle adnate to upper petal along margins in lower 3 mm, nectary basal, pulvinate; anthers ± 0.25 mm long, yellow. *Ovary* dorsoventrally flattened, lanceolate, 4×2 mm, green, sparsely and obscurely papillate; style straight or slightly curved, ± 1 mm long; ovules biseriate, ± 8 per placenta. *Fruit* pendent, dorsoventrally compressed, lanceolate, $(5\text{--})9\text{--}12 \times 2\text{--}3$ mm, dehiscent from base to $\pm$ halfway, remaining attached to replum (placenta) in distal half, several-seeded. *Seeds* lenticular, $0.6\text{--}0.8$ mm diam., glossy black, obscurely scalariform-colliculate. $2n = \pm 32$ (Lidén 1986). *Flowering time*: (August) September to October. Figure 4.

Distribution and habitat: occurs among bushes in seasonally moist, sheltered situations in coastal and inland scrub up to $\pm 1\,000$ m, from the Bokkeveld Escarpment through the southwestern and southern Cape and into the Eastern Cape as far as Port Elizabeth, Port Alfred and Grahamstown (Figure 5). The species usually grows in fine-grained clay or loamy, granite-derived soils but sometimes in neutral sands, often on south-facing slopes that are shaded in the afternoon. On nutrient-poor sandstone soils plants have been recorded as favouring richer, nitrified hyrax middens.

Diagnosis and relationships: *Cysticapnos cracca* is recognized by its lanceolate, blade-like capsules, $10\text{--}12 \times 2\text{--}3$ mm, containing numerous seeds in two peripheral rows. The pericarp dehisces from the base, with the two halves peeling away but remaining attached in the distal half. In general form and dehiscence they are very similar to those of *C. pruinosa*, but the latter has larger, $\pm$ quadrate capsules, $15\text{--}17$ mm long, that are distinctly flexed upwards in the distal half, with obscurely scalloped margins. The racemes in *C. cracca* are almost invariably sessile, with flowers smaller than those of *C. pruinosa* ($6.0\text{--}6.5$ mm vs $7\text{--}8$ mm) and generally fewer per raceme (mostly up to 15 vs more than 15). Vegetatively *C. cracca* is readily distinguished from *C. pruinosa* by its annual habit, less finely divided leaves, and yellow vs clear sap.

Cysticapnos cracca is most likely to be confused with *C. vesicaria*, with which it co-occurs in parts of the southwestern Cape. Although typically smaller and more compact than *C. vesicaria*, *C. cracca* is otherwise almost indistinguishable in foliage, both species having broadly obovate, deeply 2- or 3-lobed ultimate leaf segments. The sap of *C. cracca*, however, is distinctly yellow, staining the skin bright orange, whereas that of *C. vesicaria* is clear. The two species are readily distinguished in flower and fruit, *C. cracca* having smaller, less prominently winged flowers and flattened, non-inflated capsules. Although *C. cracca* is typically found in heavier, clay soils, with *C. vesicaria* favouring deep coastal sands and gritty granite-derived soils, the two species have been recorded growing together in several places throughout their area of sympatry.

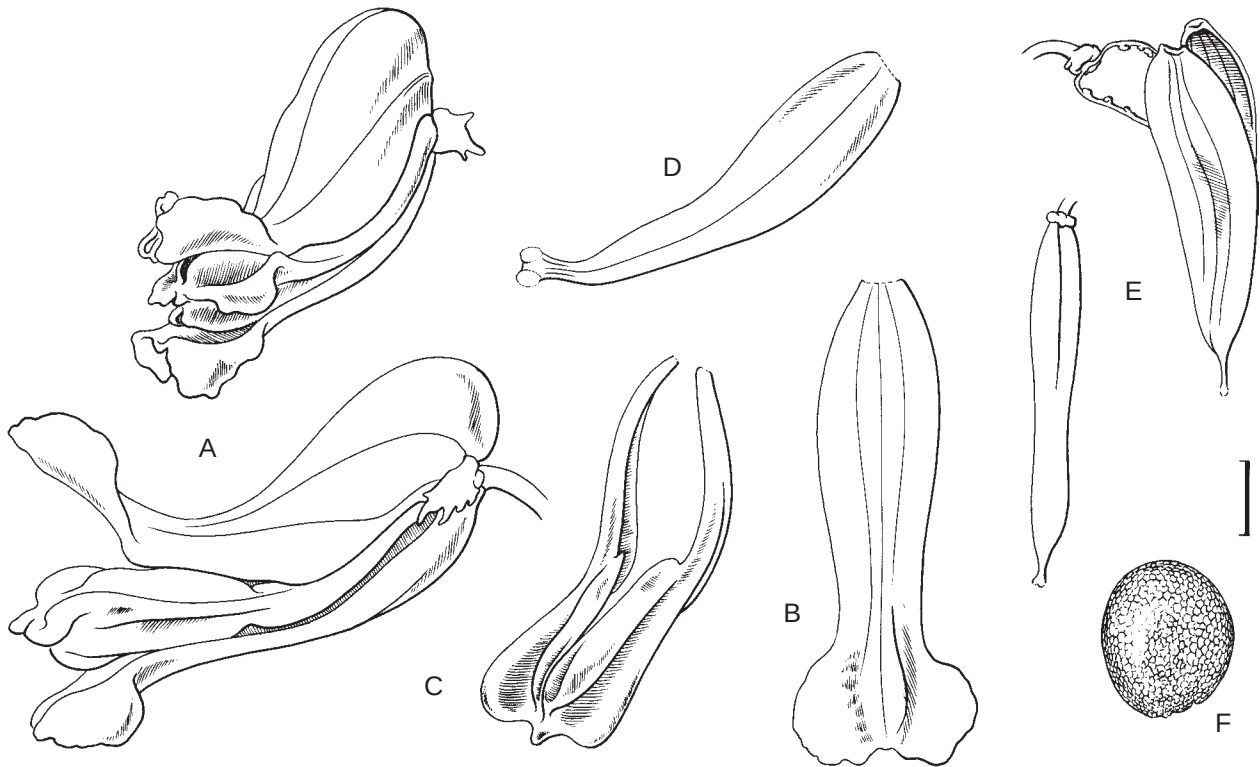


FIGURE 4.—*Cysticapnos cracca*: A, flower, front and lateral views; B, lower outer petal; C, inner petals; D, gynoecium, lateral view; E, mature fruit, lateral view before dehiscence and dorsal view after dehiscence; F, seed. Scale bar: A–C, 10 mm; E, 2.5 mm; F, 0.4 mm. Artist: John Manning.

History: *Cysticapnos cracca* was first collected by the German apothecary Carl Bergius, who arrived at the Cape in 1815. He almost certainly gathered the specimens in the immediate surrounds of Cape Town itself, and as he died here a few years later, at the beginning of 1818 (Gunn & Codd 1981), his collection must date from this three-year period. The species was described several years later in the genus *Corydalis* by the German botanists Ludolf von Chamisso and Diederich von Schlechtendal (1826) but was later transferred by Bernhardt (1838) to his new genus *Phacocapnos*, which he distinguished from *Corydalis* primarily on the lack of an aril or strophiole on the seed. This treatment was not followed by Harvey (1894) but was adopted by later botanists. At the same time Bernhardt (1838) described a later collection from Enon, north of Port Elizabeth, made by the German collector Johann Drège in 1828 as the new species *P. dregeanus* on the basis of its acute rather than obtuse fruits. As subsequently concluded by Harvey, this purported difference is not significant.

3.2. *Cysticapnos pruinosa* (E.Mey. ex Bernh.) Lidén in *Opera Botanica* 88: 106 (1986). *Phacocapnos pruinosa* [as *pruinosa*] E.Mey. ex Bernh.: 664 (1838); Hutch.: 110 (1921). *Corydalis pruinosa* (E.Mey. ex Bernh.) Harv.: 17 (1894). Type: South Africa, [Eastern Cape], 3027 (Lady Grey): Witberg [Witteberge], (–DA), 4000'–5000' [1 200–1 500 m], November without year [1832], Drège 3846 133 (I, a) (MO, holo.!; B!, BOL!, PRE!, S, iso.).

Tufted perennial with fleshy taproot, and climbing stems up to 1 m, with clear sap. Leaves bipinnately compound, ultimate segments broadly obovate, 2- or 3-lobed almost to base; terminal segments of upper leaves trans-

formed into tendrils. **Inflorescence** pedunculate, up to 160 mm long in fruit, 14–35-flowered, sometimes bearing 1 or 2 reduced leaves below; pedicels suberect and slightly curved outwards, 1–2 mm long; bracts recurved, lanceolate, 1.5–2.0 × 0.5–0.75 mm, irregularly toothed. **Flowers** pale pink with dark reddish green gibbæ. **Sepals** ovate, 2 × 1.5 mm, irregularly toothed, basally auriculate. **Petals**: outer petals naviculate-spathulate, prominently clawed, 7–8 × 0.8–1.0 mm, apically winged and 3–4 mm wide, wings patent, ± 1.5 mm wide, upper saccate at base, sac 3–4 mm deep; inner petals 5–6 mm long, claw ± 2 mm long, adnate to upper petal in lower 1 mm, blade inflated, ellipsoid, 3–4 × 1.5 mm, with papillate dorsal crest ± 1 mm wide. **Stamens**: filament bundles lanceolate, 3.5–4.0 × 1.2 mm, upper bundle adnate to

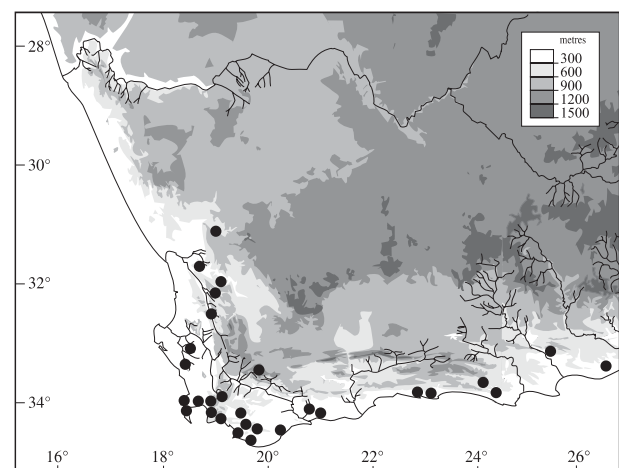


FIGURE 5.—Known distribution of *Cysticapnos cracca*.

upper petal along margins in lower 1 mm, nectary elongate-pulvinate, decurrent up lower half of spur; anthers ± 0.25 mm long, yellow. *Ovary* dorsoventrally flattened, lanceolate-quadrate, 4×1.2 mm, green; style straight, suberect, ± 0.7 mm long; ovules biseriate, ± 9 per placenta. *Fruit* pendent, dorsoventrally compressed, lanceolate-quadrate, $(12\text{--})15\text{--}25 \times 6\text{--}7$ mm, flexed upwards in distal half, margins obscurely scalloped-dentate at maturity, dehiscing from base to $\pm$ halfway, remaining attached to replum (placenta) in distal half, many-seeded. *Seeds* lenticular, $1.0\text{--}1.5$ mm diam., glossy black, scalariform-colliculate peripherally. $2n = \pm 32$ (Lidén 1986). *Flowering time*: December to February. Figure 6.

Distribution and ecology: a montane and subalpine species, distributed along the eastern escarpment of South Africa between 1 200 and 3 000 m, from the Koueveldberge west of Graaff-Reinet northwards through the Drakensberg Mountains of Eastern Cape and KwaZulu-Natal to Harrismith and westwards across the higher-lying parts of Lesotho to the Leribe Plateau (Figure 7), with isolated northern outliers along the eastern escarpment in Mpumalanga around Wakkerstroom and Ermelo and on the Mauchsberg near Lydenburg. *Cysticapnos pruinosa* typically grows in gritty, basaltic soils, scrambling among bushes and grasses on mountain slopes and in scree, in rocky boulder beds in drainage lines, or along mountain streams. It is the only member of the tribe Discocapninae to occur in the summer rainfall region.

The species has previously been regarded as an annual but excavation of several individuals confirms that it is perennial. Seedlings form the characteristic fleshy taproot within their first year but appear to flower only from the second season. Older plants develop a taproot several millimetres in diameter, and produce a crown with multiple growing points, from which new shoots arise. These, like the seedlings, seem not to flower in their first season, accumulating old leaf bases along the subterranean portion. Plants die down in winter to the crown and resprout in the spring.

The species is used medicinally by the Sotho, among whom it is known colloquially as *Musa pelo oa noka* (the river comforter), literally 'the one who puts the heart (of the river) right'. It is taken as a relief for sorrow, especially in times of bereavement (Dieterlen 1873).

Diagnosis and relationships: *Cysticapnos pruinosa* is distinguished by its perennial habit with a fleshy taproot, and by its finely divided, almost carrot-like leaves. Other species of *Cysticapnos* are annuals with a slender, almost fibrous taproot and broader, $\pm$ elliptical ultimate leaflet segments. The elongate, floriferous racemes of *C. pruinosa* produce up to 35 relatively large flowers, 7–8 mm long, with papillate rather than smooth dorsal crests on the lateral petals, and lanceolate-quadrate fruits with a distinctive transverse flexure. The clear, rather than yellow, sap is shared with *C. cracca* and with species of *Fumaria*.

History: one of several South African Fumariaceae collected by the German plant hunter Johan Drège, the species is based on his collection from the mountains around Lady Grey in Eastern Cape. Although the collection is undated as to year, his itinerary indicates that

he was in this area in late 1832 and early 1833 (Gunn & Codd 1981). Ernst Meyer, the German botanist who dealt with Drège's collections, intended describing the species in the genus *Corydalis* but his name remained unpublished and it was left to Bernhardt to formally describe the species in his new genus *Phacocapnos*, which he distinguished from *Corydalis* by the lack of an aril or strophiole on the seeds. The Bernhardt herbarium formed the basis for the Missouri Botanical Garden herbarium and the specimen there, which is marked as part of the Bernhardt Herbarium, is thus appropriately recognized as the holotype.

3.3. *Cysticapnos vesicaria* (L.) Fedde in Repertorium specierum novarum regni vegetabilis 19: 287 (1924); Lidén: 106 (1986). *Corydalis vesicaria* (L.) Pers.: 269 (1806). *Fumaria vesicaria* L.: 701 (1753). Type: South Africa, without locality or date, LINN881.16 (LINN, holo.).

C. cirrhosa Moench: 52 (1794), nom. illeg. superfl. a *Fumaria vesicaria* L.

Climbing annual up to 2 m, with clear sap. *Leaves* bipinnately compound, ultimate segments broadly obovate, 2- or 3-lobed almost to base, lobes narrowly elliptical to obovate; terminal segments transformed into tendrils. *Inflorescence* sessile (lowest flower basal), 10–60(–80) mm long, (1)2–7-flowered; pedicels suberect, curved outwards apically, 2–8 mm long, elongating to 25 mm in fruit; bracts spreading, obovate-cuneate, $2.0\text{--}2.5 \times 1.0\text{--}1.5$ mm, apically toothed. *Flowers* pale pink, upper petal with dark reddish mark at base of wing, inner petals translucent. *Sepals* sagittate, $1\text{--}2\text{--}(3) \times 0.5\text{--}1.0\text{--}(2.0)$ mm, irregularly toothed. *Petals*: outer petals naviculate-spathulate, $7\text{--}9\text{--}(13) \times 2\text{--}3$ mm, winged in outer half, wings reflexed, $2\text{--}4\text{--}(5)$ mm wide, upper petal rounded at base; inner petals 6–7 mm long, claw $1.5\text{--}2.0$ mm long, adnate to upper petal in lower 1 mm, blade ellipsoid, inflated, $4.5\text{--}5.0 \times 1$ mm, with inflated dorsal crest $1.5\text{--}2.0$ mm wide. *Stamens*: filament bundles broadly lanceolate, $3.5\text{--}4.0 \times 1.5$ mm, upper bundle adnate to upper petal along margins in lower 1 mm, nectary basal, pulvinate; anthers ± 0.25 mm long, yellow. *Ovary* ovoid, 3×1.5 mm, green; style geniculate-sigmoid, ± 0.5 mm long; ovules 4-seriate, 30–40 per placenta. *Fruit* pendulous on elongated pedicel, heterocarpic, ovoid, usually inflated and $(10\text{--})20\text{--}25 \times (5\text{--})15\text{--}20$ mm, sometimes compressed and not inflated, then 4–10 $\times$ 3–5 mm, exocarp splitting longitudinally for entire length, mesocarp usually aerenchymatous, endocarp remaining attached to exocarp by radiating threads, rupturing irregularly, many-seeded, rarely mesocarp not developing and fruits then much smaller, $5\text{--}10 \times 4\text{--}5$ mm. *Seeds* lenticular, $1.0\text{--}1.5 \times 0.8\text{--}1.3$ mm diam., excavated on faces, glossy black, obscurely colliculate and almost smooth. $2n = 28, \pm 30$ (Lidén 1986). *Flowering time*: mainly August to early October but as early as June in the Little Karoo. Figure 8.

Distribution and ecology: common and widely distributed from southern Namibia through Namaqualand and the southwestern Cape to the Little Karoo around Oudtshoorn but apparently absent from the Knersvlakte (Figure 9). The species usually occurs in coarse-grained soils, mainly coastal sands in fynbos and coastal scrub or gritty, granitic soils in renosterveld.



FIGURE 6.—*Cysticapnos pruinosa*: A, portion of flowering stem; B, base of plant; C, infructescence; D, flower, front and lateral views; E, section through spur; F, lower outer petal; G, inner petals; H, gynoecium, lateral and three-quarter views; I, seed. Scale bar: A–C, 10 mm; D–G, 1 mm; H, 0.5 mm. Artist: John Manning.

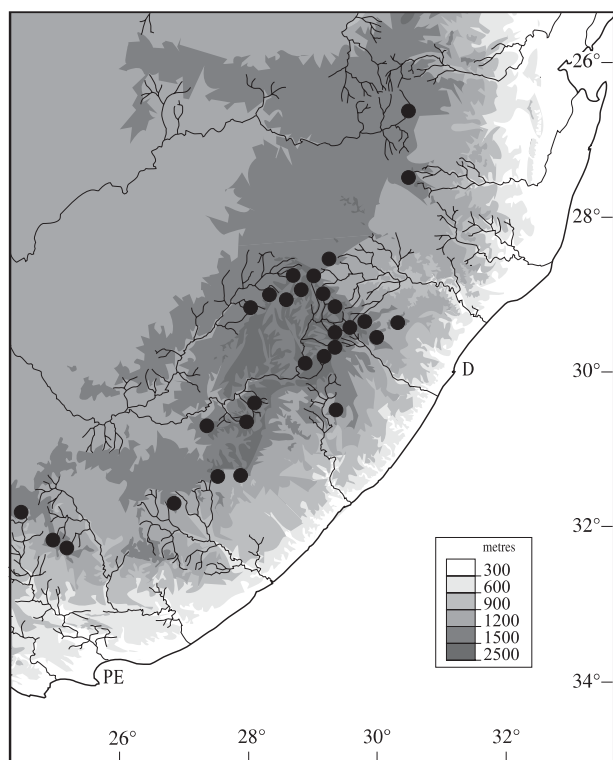


FIGURE 7.—Known distribution of *Cysticapnos pruinosa*.

Diagnosis and relationships: although similar to *Cysticapnos cracca* in foliage, *C. vesicaria* is distinguished from this and other species by the basally geniculate style and by its $\pm$ inflated, bladder-like fruit, mostly $20\text{--}25 \times 15\text{--}20$ mm. This unique fruit results from the development of a thick, highly aerenchymatous, spongy mesocarp between the papery exo- and endocarps. Even at flowering the ovary wall is clearly 3-layered. At maturity the exocarp splits longitudinally but remains attached to the endocarp by the radiating, thread-like vascular bundles, and the seeds are released through irregular rupturing of the endocarp. In some fruits, however, the mesocarp fails to expand and the capsules remain small and compressed, measuring just $4\text{--}10 \times 3\text{--}5$ mm. The seeds in these small capsules are quite normal and the same plant may produce both dwarf and normal fruits. These flattened capsules are strikingly similar to those of *C. cracca* and *C. pruinosa*. The clear, watery sap is shared with *C. pruinosa*.

Heterocarpy in *Cysticapnos vesicaria* was first noticed and reported by Fedde (1924), and later by Hilliard & Burtt, who recorded that ‘small fruits, not inflated but with ripe seeds, [are] sometimes present on [the] same raceme [as normal inflated fruits]’ (Hilliard & Burtt 13025, NU). Dwarf, flattened fruits have been recorded throughout the range of the species and are a regular feature of the species. They have no taxonomic significance although they have caused confusion in the past. *Corydalis burmannii* Eckl. & Zeyh. ex Harv. was based on plants with such dwarf fruits, and a cultivated plant that produced a single dwarf fruit formed the basis of *Cysticapnos parviflora* Lidén.

The species is typically few-flowered, with 1–4 flowers borne on short racemes up to 45 mm long. The flowers are mostly 7–8 mm long, with the upper and lower

petal wings 2–3 mm wide. Populations from the northern part of the range, in Namaqualand and the Richtersveld, however, have up to seven, mostly larger flowers borne in racemes 20–80 mm long. In these plants the outer petals may reach 10–12 mm long with apical crests 3–5 mm wide. These northern forms are treated here as subsp. *namaquensis*.

History: the first of the southern African Fumariaceae to be named, *Cysticapnos vesicaria* was described in the genus *Fumaria* by Carl Linnaeus (1753). The identity of the original collector is not known but the species was soon in cultivation in Europe and became known to later botanists under the name *Cysticapnos africana*, based on an illustration of the very distinctive fruit reproduced in Gaertner’s (1791) *De fructibus et seminibus plantarum*. It was only in the early decades of the twentieth century that Fedde (1924) resuscitated the use of the earlier name, *C. vesicaria*, in an article in which he first identified the existence of marked heterocarpy in the taxon. This led him to suspect that Harvey’s (1894) *Corydalis burmannii* was nothing more than a smaller-fruited form of *C. vesicaria*, an opinion that has now been vindicated by further observations of plants in the field. This small-fruited form was still recognized by Lidén (1986) under the illegitimate name *Cysticapnos grandiflora*. The various forms of *C. vesicaria* distinguished by Fedde (1924) on the basis of the size of the leaf segments and flowers represent nothing more than the normal variation in leaf and floral development evident even within individuals in the same population.

Plants thought to have originated from Alexandria in Egypt were cultivated in Europe under the unpublished name *Cysticapnos alexandrina*. Although thought by Fedde (1924) to have been validated by Don, this is not in fact the case as Don (1831) indicated quite clearly his opinion that the plants in question were not distinct from *C. africana*, and the name thus remains invalid (McNeill *et al.* 2006: Art 34:1).

Key to subspecies

- 1a Raceme 10–20(–45) mm long, 1–4-flowered; outer petals 7–9 mm long with wings 2–3 mm wide; plants from south-western and southern Cape subsp. *vesicaria*
- 1b Raceme (20–)30–80 mm long, 3–7-flowered; outer petals 9–13 mm long with wings 3–5 mm wide; plants from Namaqualand and southern Namibia. subsp. *namaquensis*

3.3a. subsp. *vesicaria*

Cysticapnos africana Gaertner, *De fructibus et seminibus plantarum* 2: 161 (1791); Harv.: 16 (1894); Hutch.: 110 (1921). Type: Gaertner: 161, t. 115 (1791), icono.!

Corydalis burmannii Eckl. & Zeyh. ex Harv.: 17 (1894). *Phacocapnos burmannii* (Eckl. & Zeyh. ex Harv.) Hutch.: 110 (1921). Type: South Africa, [Western Cape], Saldanha Bay and near Brackfontein, Clanwilliam, Ecklon & Zeyher 23 (SAM, lecto.!, designated by Goldblatt & Manning (2000); B!, MO!, iso.).

Cysticapnos vesicaria forma *brevilobus* Fedde: 287 (1924), syn. nov. Type: South Africa, [Western Cape], Stellenbosch and Swellendam, without date, Ecklon 21 (B, lecto.!, here designated).

Cysticapnos vesicaria forma *longilobus* Fedde: 287 (1924), syn. nov. Type: South Africa, [Western Cape], Brakdam, August 1897, R. Schlechter 11131 (B, lecto.!, here designated; MO, iso.).

Cysticapnos vesicaria forma *latilobus* Fedde ms. (without collector or date, B).

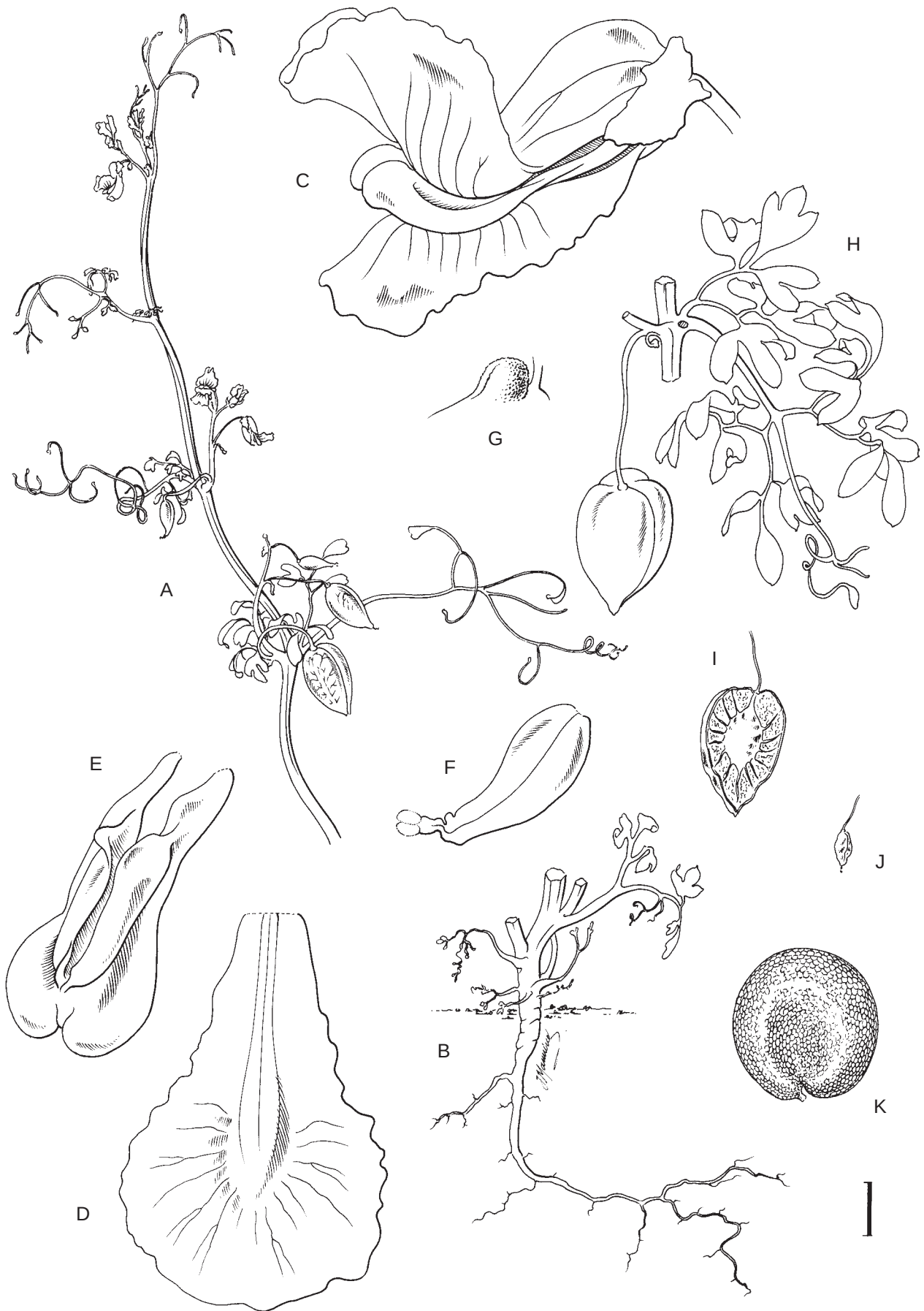


FIGURE 8.—*Cysticapnos vesicaria* subsp. *vesicaria*: A, portion of flowering stem; B, base of plant; C, flower, lateral view; D, lower outer petal; E, inner petals; F, gynoecium, lateral view; G, detail of nectary; H, infructescence (nearside lower leaf segment omitted); I, half normal fruit; J, dwarf fruit; K, seed. Scale bar: A, B, H–J, 10 mm; C–G, 1 mm; K, 0.5 mm. Artist: John Manning.

Cysticapnos alexandrina Link & Otto, nom. nud.

Cysticapnos grandiflora E.Mey.: 95 (1844), nom. nud.

Cysticapnos grandiflora [Bernh.] sensu Lidén: 106 (1986), nom. nud. [cited as *C. grandiflora* Bernh. in *Linnaea* 12 (as '13') by Lidén: 664 (1986), but not mentioned therein].

Raceme 10–20(–45) mm long, 1–3(4)-flowered. Outer petals 7–9 mm long with wings 2–3 mm wide.

Distribution and ecology: widespread through the southwestern and southern Cape, from the northern Bokkeveld Plateau southwards along the west coast and the inland mountains of the southwestern Cape as far east as Still Bay on the coast and Oudtshoorn in the Little Karoo (Figure 9). Plants are most commonly found in sandy soils in fynbos and thicket, especially along the coast, but inland populations occur on finer-grained clay or limestone soils in renosterveld.

The typical subspecies is characterized by short, 1-4-flowered racemes and relatively small flowers, 8–10 mm long, borne close to the stem and thus relatively inconspicuous.

3.3b. subsp. **namaquensis** J.C.Manning & Goldblatt, subsp. nov.

Cysticapnos parviflora Lidén: 106 (1986), syn. nov. Type: South Africa, Northern Cape, 3018 (Kamiesberg): Farm Kamagap, 10 km NE of Bitterfontein on Kliprand road, (–CC), 10 September 1974, *Nordenstam & Lundgren* 1803 (S, holo.!).

Racemus (20–)30–40(–80) mm longus, 3–5(–7)-flora, alis petali externis 3–5 mm latis.

TYPE.—Northern Cape, 3018 (Kamiesberg): Langkloof, renosterveld near river, 735 m, (–CA), 7 September 2006, *Snijman* 2081 (NBG, holo.; K, iso.).

Raceme (20–)30–40(–80) mm long, 3–5(–7)-flowered. Outer petals 9–13 mm long with wings 3–5 mm wide.

Distribution and ecology: widespread through the higher-lying parts of Namaqualand, from Nuwerus northwards into the Richtersveld, and into southern Namibia on the Numaisspitze at the southern edge of the Huib Hock Plateau (Figure 9). Plants grow in sandy or gritty soils, often along seasonal washes and watercourses.

This subspecies is distinguished from subsp. *vesicaria* by the mostly longer, more floriferous racemes bearing 3–7 flowers. Populations between Garies and Springbok have especially large flowers, 10–15 mm long, and constitute a particularly attractive form of the species in which the racemes of showy flowers project conspicuously above the stems that twine through the upper twigs of supporting shrubs. The collections from southern Namibia, in contrast, have the small flowers of subsp. *vesicaria* but their longer, more floriferous racemes are typical of subsp. *namaquensis*.

A cultivated plant grown in Europe in 1974 from seed collected between Bitterfontein and Kliprand produced unusually small flowers and a single dwarf fruit, and was described as the new species *Cysticapnos parviflora* by Lidén but is evidently nothing more than a poorly developed individual of this subspecies. The wild collection has the relatively many-flowered racemes and large flow-

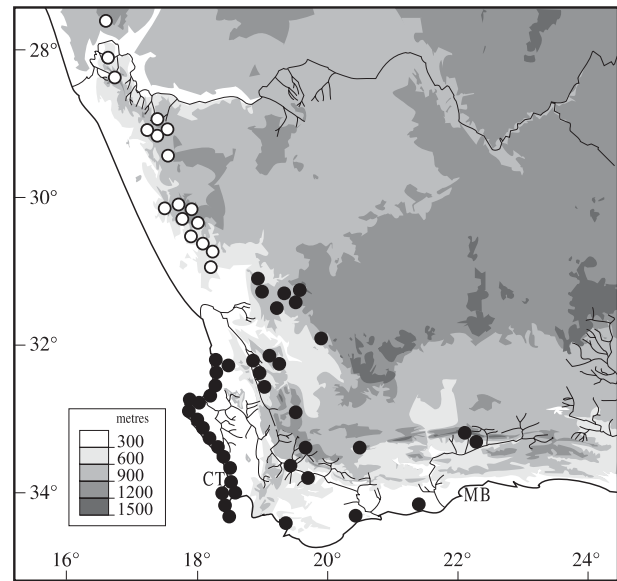


FIGURE 9.—Known distribution of *Cysticapnos vesicaria* subsp. *vesicaria*, ●; and *C. vesicaria* subsp. *namaquensis*, ○.

ers typical of subsp. *namaquensis* with the petal wings up to 7 mm wide, compared to 2 mm in the cultivated material (Lidén 1986). The seeds of these cultivated plants, which measured 0.8 mm in diameter, were contrasted against the larger seeds 1.3 mm in diameter of *C. grandiflora* (Lidén 1986) but seed size is variable in *C. vesicaria* and can range from 0.8–1.5 mm in diameter within a single collection (e.g. *Buys* 474, *Rosch* 547). This apparent difference in seed size is thus not significant. No further material matching the cultivated plants, from which much of the description and illustrations were based, has been collected despite the fact that the type locality is on a well-travelled road through Namaqualand.

History: although mostly quite distinct from the southern forms of the species in the wild, the larger-flowered northern populations have not been recognized taxonomically until now.

II. Subtribe **Fumariinae**

Scandent annuals (rarely perennial) with 2–4-pinnate leaves, lacking tendrils. *Racemes* pedunculate. *Flowers* white to pink, or yellow, upper petal spurred. *Style* deciduous; stigma with two papillae. *Fruit* a hard-walled nutlet, one-seeded, indehiscent, usually with two apical germination pores.

Four genera: *Cryptocapnos*, *Fumaria*, *Fumariola* and *Rupicapnos*. Mainly Mediterranean to central Asia, also North and East Africa, and the Himalayas.

4. **Fumaria** L., *Species plantarum*: 699 (1753). Type species: *Fumaria* L.

Brittle, semisucculent, glabrous, erect or diffuse annuals; stems quadrate, with obscure unicellular papillae along angles; sap watery, clear. *Leaves* alternate, 2–4-pinnately compound, primary divisions alternate or opposite; ultimate leaflets linear to obovate, without tendrils but sometimes petiolule and rachis prehensile. *Inflorescence* sessile or pedunculate, terminal but leaf-

opposed through rapid growth of axillary bud, racemose, pedicels often thickening in fruit; bracts scale-like, petaloid, irregularly toothed. *Flowers* zygomorphic, bilabiate, pink, unscented. *Sepals* 2, lateral, much shorter than petals, scale-like, petaloid, often irregularly toothed. *Petals* 4 in 2 series; outer petals larger, naviculate-spathulate, laterally winged apically, upper spurred at base, inner petals apically connate, clawed, limb inflated with dorsal crest, claw basally adnate to upper petal. *Stamens* 6, diadelphous in abaxial and adaxial bundles of 3; filaments of each bundle fused, lanceolate, membranous, clasping ovary, upper filament cluster adnate to margins of dorsal petal basally to form small chamber, with nectary decurrent on dorsal petal into spur. *Ovary* subglobose; ovules 1 or 2; style longer than ovary, $\pm$ slightly upcurved or flexed upwards apically, deciduous; stigma compressed, 2-lobed. *Fruit* $\pm$ erect or pendulous, subglobose or obreniform, smooth or rugulose, indehiscent and dropping entire, exocarp papery, endocarp hard and bony with paired apical germination pores. *Seed* solitary, lenticular, thin-walled, without elaiosome.

$\pm$ 50 spp., Mediterranean to India and east tropical Africa, mainly North Africa and Spain.

Key to naturalized species

- 1a Peduncle longer than raceme; pedicels recurved, 3–5 mm long; sepals large, 4–6 mm long 4.1 *F. capreolata*
- 1b Peduncle shorter than raceme; pedicels stiffly suberect or spreading, sometimes recurving slightly in fruit, 1.5–2.5 mm; sepals small, 0.5–3.0 mm long:
 - 2a Leaves not as finely divided, parsley-like, ultimate segments oblanceolate-obovate (rarely $\pm$ linear); flowers pink and purple, 7–10 mm long, including spur; bracts 1.0–1.5 mm long, half to three-quarters as long as pedicels 4.2 *F. muralis*
 - 2b Leaves finely divided, almost dill-like, ultimate segments linear; flowers white turning pink, and purple, $\pm$ 5 mm long, including spur; bracts 2–3 mm long, as long as or longer than pedicels 4.3 *F. parviflora*

4.1. *Fumaria capreolata* L., Species plantarum: 701 (1753); Sell: 256 (1964); Lidén: 67 (1986); Walsh & Norton: 407 (2007). Type: France, prope Olbyam Galilae Narbonense (*UPS-LINN74560*, holo.).

Sprawling or scandent, branching annual up to 1 m. *Leaves* bipinnately compound, rachis sometimes flexuous, ultimate segments obovate, dissected almost to base, lobes elliptical, apiculate-aristate. *Inflorescence* pedunculate, up to 80 mm long in fruit; raceme shorter than peduncle, 10–25(–35)-flowered; pedicels recurved, 3–5 mm long, apically thickened in fruit; bracts patent, not clasping pedicel, linear-lanceolate, $2.5\text{--}4.0 \times 0.5\text{--}0.8$ mm. *Flowers* creamy white or pale pink with dark reddish tips. *Sepals* peltate, ovate, $4\text{--}6 \times 2.5\text{--}4.0$ mm, irregularly toothed. *Petals*: outer petals naviculate, upper spathulate and apically short-winged, wings reflexed, $\pm$ 0.5 mm wide, spurred at base, spur compressed saccate, $2.5\text{--}3.5$ mm long, lower linear with rudimentary apical wings, $8\text{--}9 \times 1.0\text{--}1.5$ mm; inner petals $7\text{--}9$ mm long, claw $\pm$ 2 mm long, adnate to upper petal in lower 1 mm, blade inflated, narrowly oblong, $5\text{--}7 \times 1$ mm, with fleshy dorsal crest $\pm$ 0.5 mm wide. *Stamens*: filament bundles lanceolate-attenuate, $5\text{--}6 \times 1$ mm; anthers $\pm$ 0.25 mm long, yellow. *Ovary* subglobose, 1.5 mm diam., green; style slightly curved, 4–5 mm long, green, deciduous. *Fruit* globose, $2.0\text{--}2.5$ mm diam., indehiscent and drop-

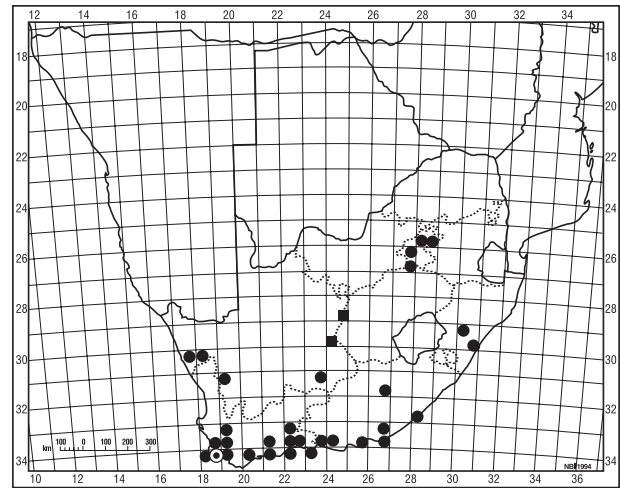


FIGURE 10.—Known distribution in southern Africa of *Fumaria capreolata* and *F. muralis*, ○; *F. muralis*, ●; and *F. parviflora*, ■.

ping entire, brown, exocarp membranous, finely tuberculate or almost smooth, endocarp woody with small hour-glass-shaped apical pit. *Seed* not seen. *Flowering time*: September to October.

Distribution and ecology: native to the Mediterranean and southwestern Europe but widely naturalized in warmer temperate countries, including southern Australia. Known in South Africa from a single collection made near Somerset West in Western Cape in 1952 (Parker 4818) (Figure 10), it is so far at most an occasional adventive here.

4.2. *Fumaria muralis* Sond. ex W.D.J.Koch, Synopsis florae germanicae et helveticae, edn 2, part 3: 1017 (1845); Sell: 257 (1964); Lidén: 78 (1986); Walsh & Norton 408 (2007). Lectotype designated by Walsh: 496 (1992): Germany, Hamburg in muris, July 1844, Sonder s.n. (*MEL1584466*, lecto.).

4.2a. subsp. *muralis*

F. officinalis var. *grandiflora* DC.: 135 (1824). Type: South Africa, without precise locality or collector (G-BU, holo.).

F. officinalis var. *capensis* Harv.: 18 (1894), syn. nov. Type: South Africa, [Western Cape], Witzenberg, without date, Ecklon & Zeyher 25 (TCD, holo.; PRE, SAM, iso.!).

Sprawling or scandent, branching annual up to 0.5 m, with clear sap. *Leaves* bipinnately compound; rachis sometimes flexuous; ultimate segments obovate, dissected almost to base, lobes elliptical (rarely $\pm$ linear), apiculate-aristate, terminal segment rarely without a blade. *Inflorescence* pedunculate, up to 30 mm long in fruit, 3–12-flowered; pedicels suberect or spreading, $2.0\text{--}2.5$ mm long, thickened, firm and sometimes slightly recurved in fruit; bracts erect, clasping pedicel, $1.0\text{--}1.5 \times 0.5$ mm, irregularly toothed. *Flowers* pale to deep pink with dark reddish tips. *Sepals* peltate, ovate, $2\text{--}3 \times 1.5\text{--}2.0$ mm, irregularly toothed. *Petals*: outer petals naviculate, $5\text{--}7 \times 1.0\text{--}1.5$ mm, upper petal spathulate and apically short-winged, wings reflexed, $\pm$ 0.5 mm wide, spurred at base, spur compressed saccate, $2.0\text{--}3.5$ mm long, lower petal linear with rudimentary apical wings; inner petals $5\text{--}7$ mm long, claw $\pm$ 1.5 mm long, adnate to upper petal in lower 1 mm, blade inflated, nar-

rowly oblong, 4–5 × 1 mm, with fleshy dorsal crest ± 0.5 mm wide. *Stamens*: filament bundles lanceolate-attenuate, 5–6 × 1 mm; anthers ± 0.25 mm long, yellow. *Ovary* subglobose, 1.5 mm diam., green; style ± straight or slightly curved, 4–5 mm long, green, deciduous. *Fruit* suberect, globose, 2.0–2.5 mm diam., indehiscent and dropping entire, brown, exocarp membranous, finely tuberculate or ± smooth, endocarp woody with small hourglass-shaped apical pit. *Seed* depressed-subglobose, 1.5–2.0 mm diam., testa membranous, containing scattered, elongate orange deposits. *Flowering time*: mainly August to October, later or earlier in gardens. Figure 11.

Distribution and ecology: native to Europe but introduced elsewhere, including Australia and New Zealand. The species is widely distributed in South Africa as a ruderal through the wetter, more temperate parts of both winter and summer rainfall regions (Figure 10). It is especially common in the southwestern and southern Cape but has also been recorded from the higher-lying Kamiesberg in central Namaqualand and into the Eastern Cape, in KwaZulu-Natal between Durban and Pietermaritzburg, and in Gauteng, with isolated collections from Kimberley, Bloemfontein and Phalaborwa. It is found along the margins of cultivated lands and in fallow fields, in waste places, and as a weed in gardens. *Fumaria muralis* is essentially cleistogamous, the anthers dehiscing before the petals separate, and the style abscising from the ovary by anthesis.

The species appears to have been first collected in South Africa during the latter part of the eighteenth century by Carl Thunberg, who observed (Thunberg 1823) that it had become widely established in the southwestern Cape, both in gardens and outside of them. This very early appearance of *Fumaria muralis* makes it one of the first exotic plant species to naturalize in South Africa. Other early collections from the southwestern Cape, made during the first half of the eighteenth century, include those by Christian Ecklon & Carl Zeyher (Ecklon & Zeyher 25) and by Johann Drège (PRE24456). Collections from the end of the century by Henry George Flanagan and Alice Pegler record its occurrence in the Eastern Cape, and it had reached central Namaqualand, KwaZulu-Natal and Gauteng by the early decades of the twentieth century.

It is almost certain that *Fumaria muralis* was an accidental introduction to South Africa, probably among wheat seed brought from Europe. Species of *Fumaria* are common weeds of cereal crops in Australia and wheat was already cultivated widely in the southwestern Cape by the time that *F. muralis* was first collected in the region by Thunberg (Thunberg 1823). This mode of introduction would also explain its rapid spread through the country. The alternative, that it was a deliberate introduction, is not supported by any evidence. The small flowers of *F. muralis* make it useless as an ornamental and although the closely allied *F. officinalis* is used medicinally in Europe (Launert 1981), the absence of any mention of the species in Pappe's early treatise on South African medicinal plants (Pappe 1868) (and which included other introductions) or in the later compendium by Watt & Breyer-Brandwijk (1932), suggests that it was not introduced for medicinal purposes.

Early collections of the species from southern Africa were identified as forms of *Fumaria officinalis* L. (at that time *F. muralis* had still to be described), and even until recently *F. muralis* was often treated as a synonym of *F. officinalis*. True *F. officinalis* is characterized by more pronouncedly spatulate lower petals, and nutlets that are broader than long, apically truncate or emarginate and often obreniform in shape (Sell 1964; Lidén 1986). When pressed, green fruits of *F. muralis* may split open at the apex and thus appear to be obreniform, and this has resulted in some collections being misidentified as *F. officinalis*. Although an uncommon introduction in Australia, *F. officinalis* does not yet appear to have been recorded in South Africa.

Nomenclatural note: Harvey (1894) treated the South African material as *Fumaria officinalis* var. *capensis* Harv., based on Ecklon & Zeyher 25, and although his citation of the earlier name *F. capreolata* β. *burchellii* DC. (1824) would render his name superfluous were de Candolle's epithet to be accepted at varietal level, we interpret de Candolle's hesitant citation of the rank of his name as *F. capreolata* β? *burchellii* to be sufficient grounds for considering the name rankless and thus without priority at varietal rank (McNeil et al. 2006: Art. 52.1).

4.3. *Fumaria parviflora* Lam., Encyclopédie méthodique. Botanique 2: 567 (1788); Sell: 258 (1964); Lidén: 88 (1986); Walsh & Norton: 410 (2007). Type: In cult. Paris, of Mediterranean origin, Lamarck (P-LAM, holo.).

4.3a. var. *parviflora*

Sprawling, branching annual up to 0.5 m. *Leaves* ternately compound; primary divisions alternate or opposite, ultimate segments finely dissected to base, lobes linear, apiculate-aristate. *Inflorescence* up to 30 mm long in fruit, (7–)10–15(–22)-flowered; pedicels suberect, 1.5–2.0 mm long, thickened and firm in fruit; bracts erect, clasping pedicel, 2.0–3.0 × 0.5 mm, irregularly toothed. *Flowers* white, turning pink with age, with dark reddish tips. *Sepals* cordate, broadly ovate, 0.5–1.0 × 0.5–0.7 mm, irregularly toothed. *Petals*: outer petals naviculate, 3–4 × ± 1 mm, upper petal spatulate and apically short-winged, wings patent, ± 0.5 mm wide, spurred at base, spur compressed saccate, 1.0–1.5 mm long, lower petal linear with rudimentary apical wings; inner petals 3–4 mm long, claw ± 1.5 mm long, adnate to upper petal in lower 1 mm, blade inflated, narrowly oblong, ± 2.5 × 1 mm, with fleshy dorsal crest ± 0.5 mm wide. *Stamens*: filament bundles lanceolate-attenuate, 2.5–3.0 × 1 mm; anthers ± 0.1 mm long, yellow. *Ovary* subglobose, ± 1 mm diam., green; style flexed sharply upwards apically, ± 2 mm long, green, deciduous; ovule 1, lateral. *Fruit* suberect, globose, ± 2 mm diam, indehiscent and dropping entire, brown, exocarp membranous, finely rugose-tuberculate, endocarp woody with small hourglass-shaped apical pit at stylar end. *Seed* not seen. *Flowering time*: August to February.

Distribution and ecology: native to the Mediterranean but widely naturalized elsewhere, including Australia, where it is scattered but uncommon. In South Africa the species appears to be naturalized only in the drier western parts of the Northern Cape and Free State, where it has been recorded from Hopetown and Kimberley (Fig-

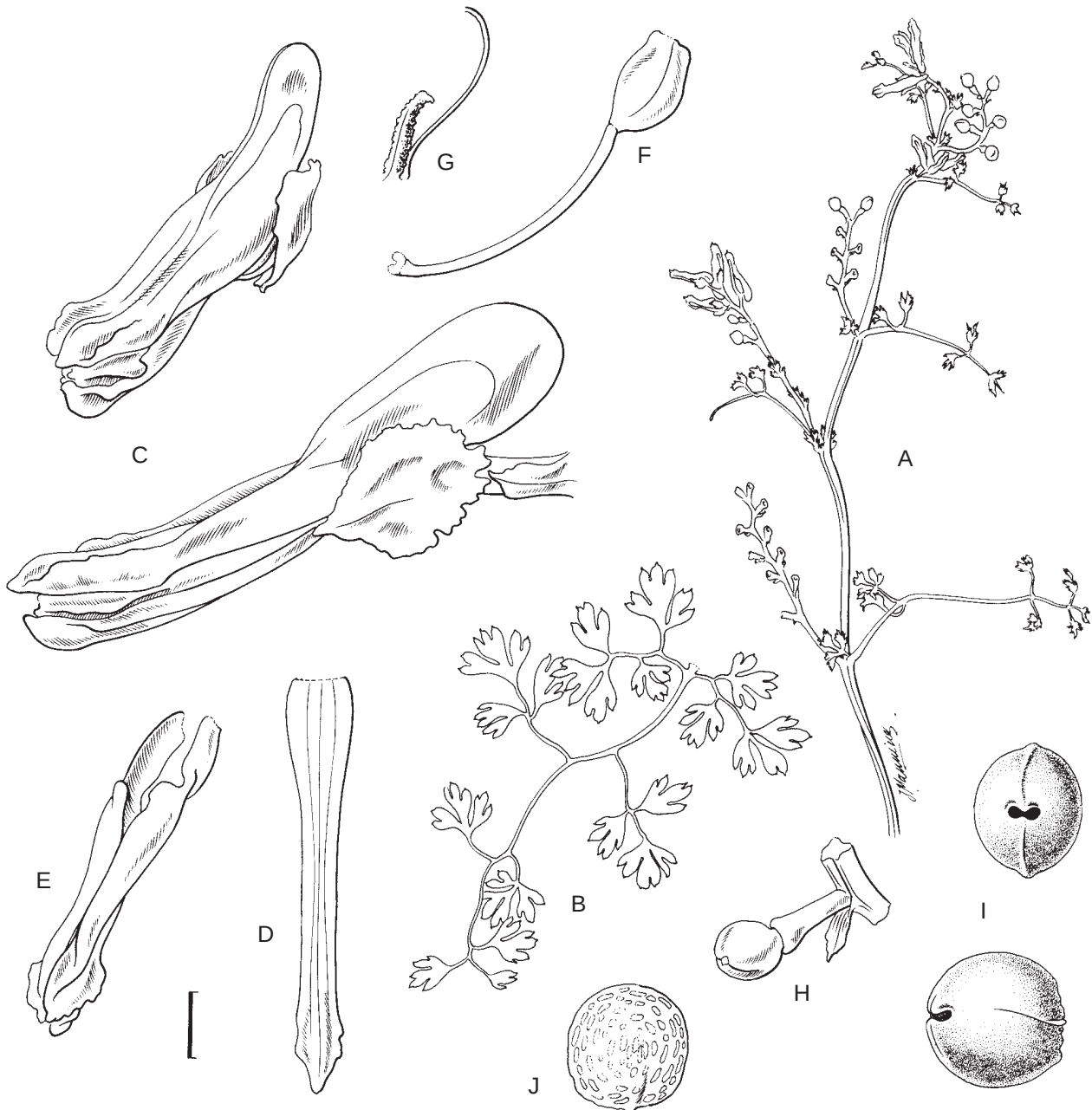


FIGURE 11.—*Fumaria muralis*: A, portion of stem; B, detached lower leaf; C, flower, three-quarter and lateral views; D, lower outer petal; E, inner petals; F, gynoecium, lateral view; G, detail of nectary; H, fruit; I, endocarp, front and dorsal views; J, seed. Scale bar: A, B, 10 mm; C–J, 1 mm. Artist: John Manning.

ure 10), typically along irrigation ditches or channels, where it is regarded as a troublesome weed, forming dense stands in wet places and choking the canals. The species is evidently a recent introduction to the country, and no records from earlier than the latter decades of the twentieth century have been seen.

Fumaria parviflora, like *F. muralis*, is essentially cleistogamous, the anthers dehiscing before the petals separate, and the style abscising from the ovary by anthesis.

OTHER SPECIMENS EXAMINED

The taxa are indicated in brackets by the number assigned to them in the text, followed by the herbarium acronym.

Abbot 4775, 5509 (3.2) MO, NH. Acocks 10477 (4.2) PRE; 14883, 16960, 17782 (2) PRE; 14950 (3.3b) PRE; 20433 (3.2) PRE; 20653, 21571, 22723 (3.1) PRE. Adamson 1936 (3.3a) BOL; 2103 (1a) BOL. Andreae 390 (3.3a) NBG. Axelsson 477 (3.3a) NBG.

Baker 6 (4.2) PRE. Balkwill, Manning & Cadman 1145 (3.2) MO, NU, PRE. Barker 1360 (3.3b) NBG; 5929 (3.3a) NBG. Baur ex Marloth 11457 (3.1) PRE. Bayer 227 (3.1) NBG; 240 (4.2) NBG. Bayliss 87 (3.2) MO. Behr 481 (4.2) PRE. Bester 2700 (3.2) NH; 3953 (3.2) PRE. Bohnen 4762 (4.2) NBG, PRE. Bolus 1003 (3.1) BOL; 4697 (1a) BOL, NBG; 2702, 8052, 12596 (3.3a) BOL; 8920 (2) PRE. Bond 509 (3.3a) NBG. Booi 132, 135 (4.2) PRE. Borchardt PRE463 (3.1) PRE. Bosenberg & Rutherford 75 (3.3a) NBG. Botes 397 (3.1) NBG. Boucher 528 (3.1) NBG, PRE; 6579 (3.3a) NBG. Braun 2224 (3.2) PRE. Bremer 281 (3.3a) PRE. Brooke 3 (3.3a) BOL. Brynard 255 (4.2) PRE. Burgers 2114 (4.2) NBG; 2933 (3.3a) NBG. Burrows 6393 (3.2) PRE. Burtt-Davy 10811 (4.2) PRE. Buys 474 (3.3a) NBG.

Cairns PRE54105 (4.2) NBG, PRE. Castelnau PRE24458 (4.2) P, PRE. Cloete & Haselau 283 (2) NBG; 285 (3.3a) NBG. Coleman 312 (3.2) PRE. Compton 2688, 24323 (2) NBG; 3508 (3.1) BOL; 6808,

17216 (3.3b) NBG; 21516 (3.2) NBG, PRE; 22296 (1a) NBG. Crosby 660 (3.3b) PRE. Cruz 54 (3.3b) NBG; 126 (4.2) NBG.

Dahlstrand 2112 (3.3a) MO, NBG, PRE; 2453 (4.2) PRE. De la Bat s.n. (3.1) NBG. De Vos 1461 (3.1) NBG. Devenish 513, 1203 (3.2) PRE. Dieterlen 873 (3.2) PRE, SAM. Dobay 65 (3.1) NBG; 66 (3.3a) NBG. Dive 104 (3.2) PRE. Drège 3847 (3.1) BOL; PRE24456 (4.2) P, PRE.

Ecklon 25 (4.2) PRE. Eliovson 35 (3.3b) PRE. Esterhuysen 231, 11226 (1a) PRE; 564, 11227 (3.1) PRE; 5539 (2) BOL; 5825 (3.1) NBG; 11848 (1a) BOL, PRE. Evrard 8934 (3.3b) PRE.

Fabian 1244 (3.2) PRE. Fellingham 236 (4.2) NBG, PRE. Flanagan 806 (4.2) PRE, SAM. Fourcade 398 (4.2) NBG; 506 (3.1) BOL, MO; 904 (1b) BOL. Fugler 101 (4.2) NBG, PRE.

Galpin 1803 (3.2) BOL; 6569 (3.2) BOL, NH, SAM; 8229 (4.2) PRE. Giess 13070 (3.3b) PRE. Giffen 710 (4.2) PRE. Gill 64 (4.2) PRE. Gillett 547, 1080 (3.1) NBG; 3380 (1a) NBG, PRE. Glass 21 (4.2) NBG. Goldblatt 1980 (3.1) MO; 2334 (3.3a) MO, PRE; 5793 (2) PRE. Goldblatt & Manning 10520, 10554 (2) NBG; 10577 (2) BOL, MO, PRE; 13016 (3.1) MO, NBG, PRE. Goldblatt & Porter 12396 (3.3a) NBG; 12421 (2) MO, NBG. Greene 1091 (3.2) NH. Grobler 38 (3.3b) PRE. Gubb KMG11151 (4.3) PRE. Guillard 597, 1079 (3.2) PRE. Guthrie 2538 (3.1) NBG.

Hahndiek 15 (3.3a) NBG. Hall 4464 (2) NBG, PRE; s.n. (3.3b) NBG. Hanekom 688 (4.2) NBG, PRE; 1189 (3.3a) NBG, PRE. Harris 30 (4.2) PRE. Harvey s.n. (1a) PRE, TCD. Haynes 1110 (1a) NBG, PRE; 1110A (3.1) PRE. Heineken 103 (4.2) PRE. Helme 2615 (3.2) NBG. Herre s.n. (3.3b) NBG. Heyns s.n. (3.3a) NBG. Hilliard & Burtt 6670 (3.2) MO, NU; 8869, 12192 (3.2) NU; 13025 (3.3a) NU, PRE; 14968 (3.2) NU, PRE. Hilton-Taylor 1185 (3.3b) NBG. Hugo 442 (3.3a) NBG; 542, 2432, 2959 (3.3a) NBG, PRE. Hutchinson 263 (3.3a) BOL, PRE; 780 (2) K, PRE.

Jacobsz 2013 (3.2) NBG.

Kemper IPC621 (3.1) NBG. Killick 2277, 4390 (3.2) PRE. Kinges 1761 (4.2) PRE. Kok & Pienaar 1214 (4.2) PRE. Kroon 38 (4.2) PRE. Kruger 513 (4.2) NBG, PRE.

Le Roux 2426 (3.3a) PRE; 2483 (3.3a) NBG, PRE; Le Roux & Ramsey 365 (3.3a) NBG, PRE. Leipoldt 20752 (2) BOL. Levyns 3217, 11320 (3.3a) BOL; 3453, 8511 (1.1a) BOL; 4065 (3.3b) BOL; 50572 (3.3a) BOL, PRE. Lewis 1905, 1906 (3.3b) SAM; 19829 (3.1) BOL. Linder 2196 (3.3a) BOL. Loubser 3457 (3.1) NBG. Low 925 (4.2) NBG, PRE; 976 (4.2) NBG; 927a (3.3a) NBG, PRE; 2799 (3.3a) NBG.

MacOwan 1247 (3.1) BOL; 1713 (3.2) SAM; SAM14025 (3.1) SAM. Maguire 288 (3.3b) NBG; 1887 (2) NBG; 1916 (3.3a) NBG. Manning 3017 (4.2) NBG. Manning, Hilliard & Burtt 16020 (3.2) E, NU. Marais 1352 (3.2) BOL, PRE. Marloth 237 (3.3a) PRE; 570 (4.2) PRE; 3612 (1a) PRE; 6773 (3.3b) NBG, PRE; 12448 (3.3b) PRE. Marsh 370 (3.3a) NBG, PRE; 399 (3.1) NBG, PRE. Matthews 901 (3.2) NBG. Mauve 2861 (4.2) PRE; 4544 (3.3a) PRE. Medley-Wood 4597, 5237 (3.2) NH. Meyer 3735 (4.2) PRE. Moffet 71 (4.2) NBG, PRE; 191 (3.3a) NBG, PRE. Mogg 1055, 11688 (4.2) PRE. Montgomery 48 (3.1) NBG. Moriarty 723 (3.3a) NBG. Muir 5 (3.3a) PRE; 6 (4.2) PRE; 2921 (3.1) PRE.

Nelson 11622 (4.2) PRE. Newnham Brothers PRE54096 (4.2) PRE. Nicolson 2102 (4.2) PRE.

O'Callaghan, Fellingham & Van Wyk 2 (4.2) NBG, PRE. Oliver 3716 (4.2) NBG, PRE; 4350 (4.2) NBG. Oliver, Tölken & Venter 475, 643 (3.3b) NBG, PRE; Olivier 90 (3.3a) NBG, PRE; 781 (4.2) NBG.

Parker 4235 (4.2) NBG; 4818 (4.1) NBG. Pearson 172, 6603 (4.2) NBG. Pegler 519 (4.2) PRE. Perry & Snijman 2289 (3.3a) NBG, PRE; 2290 (2) NBG. Phillips 1390 (4.2) SAM; 7616 (3.1) SAM; s.n. (3.3a) NBG. Phillipson 717, 1449 (3.2) PRE; 717 (3.2) MO. Phillipson & Hutchings 167 (3.2) K, MO, PRE. Pienaar 1155, 1166 (3.3b) PRE. Pillans 2859, 6921 (3.1) BOL. Potts 5133 (3.2) BOL, PRE; 2817 (4.2) PRE. Pretorius 270 (2) NBG. Purcell SAM89465 (4.2) SAM.

Rennie s.n. (3.2) NU. Roberts 3439 (3.2) PRE. Retief 651 (4.2) PRE. Rodin 1475 (3.3b) MO, PRE. Rogers 3484 (3.1) MO. Rösch 547 (3.3a) NBG; 644 (2) NBG. Rösch & le Roux 696 (3.3b) PRE; 1452 (4.2) PRE. Rourke 577 (3.3a) MO, NBG; 1114 (3.3a) MO, NBG, PRE. Roux Grootfontein 132 (4.3) PRE. Rubin 420 (4.2) PRE.

Schelp 239 (3.3b) BOL; 506 (3.2) NU, PRE; 1443 (3.2) NU. Schlechter 4596 (3.1) PRE; 4941 (3.3a) NBG, PRE; 10863 (2) MO; 10869 (2) BOL, PRE; 11060 (3.3b) BOL, MO; 11131 (3.3b) PRE. Schmidt 383

(3.3a) PRE. Schmitz 8352 (4.2) PRE; 9312 (3.2) PRE. Schönland 3636 (4.2) PRE. Schweickerdt 2569 (3.3b) PRE. Shearing 1295 (4.2) PRE. Sidey 2242 (3.1) MO. Sikhakhane & Williams 390 (3.2) NH, PRE. Smith 3027 (3.3a) PRE. Smuts s.n. PRE59122 (3.3a) PRE. Staples 217 (3.2) PRE. Steiner 529 (3.2) MO, NBG; 748 (2) NBG; 768 (3.3a) NBG; 861 (3.2) NBG; 921, 3657 (3.3b) NBG. Stewart 1903 (3.2) MO, NU. Steyn 14, 95 (4.2) PRE; 572 (3.3a) NBG; 592 (2) PRE. Strey 2823 (3.3a) PRE; 11013, 3909 (4.2) PRE. Stokoe SAM67430 (3.3a) SAM. Strid & Strid 37430, 38077 (3.3a) PRE. Symons 14553 (3.2) PRE.

Taylor 1553 (3.1) SAM; 2718 (3.3a) NBG; 3951, 8150 (4.2) NBG; 4103, 11827 (3.1) NBG; 4104, 7411 (3.3a) NBG, PRE; 7410, 7421 (3.1) NBG, PRE; 11788 (2) NBG, PRE; 11801 (3.3a) MO, NBG, PRE. Theron 1089 (4.2) PRE. Thode 5441, 5442, 6132 (3.1) NBG; 6133, 6134 (1.1a) NBG; 8267 (3.2) NBG; 9281 (3.3a) NBG; A473, A1140 (3.2) PRE; s.n./A738 (1.1b) BOL, NH, PRE; A1878 (3.1) PRE; A1958 (3.3a) NBG, PRE; A1959 (4.2) NBG, PRE; STE5670 (3.2) NH. Thompson 394, 1034 (3.3b) NBG, PRE; 1875 (3.1) NBG. Thompson & Le Roux 49 (3.3b) MO, NBG, PRE. Thorne SAM48867 (3.3b) SAM. Trauseld 365 (3.2) NU. Tyson 498, 1728 (3.2) SAM; 640 (3.3a) NBG, PRE, SAM.

Van Breda 43, 80 (3.3a) PRE. Van der Merwe 866 (4.2) PRE; 1746 (3.3a) NBG; 2557 (3.3a) PRE. Van der Walt 157 (3.3b) NBG, PRE; s.n. (3.3a) NBG. Van Jaarveld 1389 (3.3b) PRE. Van Niekerk 814 (3.1) BOL. Van Rooyen 2254 (3.3a) PRE. Van Wyk 717 (4.2) NBG, PRE; 1244 (3.3a) NBG, PRE; 1937 (3.1) NBG, PRE; 1937A (3.3a) NBG; 6305 (3.3b) PRE. Van Wyk & Abbott 12058 (3.2) PRE. Van Wyk, Winter & Tilney 3458 (3.1) PRE. Van Zyl 3122 (3.3a) NBG, PRE. Venter 9537 (3.3b) PRE. Verdoorn s.n. PRE54147 (3.1) PRE. Victor 211 (4.2) PRE. Viviers 602 (3.3a) NBG, PRE.

Walgate 295 (3.3a) NBG. Walters 2004 (4.2) NBG. Ward 606 (4.2) PRE. West 630 (3.2) PRE. Wiese 6 (4.2) NBG. Williams 3320 (4.2) NBG. Williamson 3562, 3916 (3.3b) NBG. Wilman 1475 (3.3b) BOL. Winkler 92 (4.2) NBG. Wolley Dod (3.1) BOL; 114 (1.1a) BOL. Wright 1798 (3.2) NU.

Zantovska 117 (4.2) PRE. Zeitsman & Zeitsman 1003 (3.3b) PRE; 1101 (2) PRE?; 1458 (3.2) PRE. Zeyher 4936 (3.1) BOL, SAM; PRE54116 (4.2) PRE; SAM14029 (3.3a) SAM. Zeyher, Preiss & Krauss SAM14028 (3.3a) SAM.

ACKNOWLEDGEMENTS

We are grateful to the curators and staff of the various herbaria consulted and especially those of the Berlin and Stockholm herbaria for making loans of the types in their collections available to us for study. We also thank Roy Gereau and Nick Turland for their help on nomenclature.

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Two new species of *Nemesia* (Scrophulariaceae) from arid areas of the Northern Cape, South Africa

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Keywords: Namaqualand, *Nemesia* Vent., new species, Scrophulariaceae, South Africa, Tanqua Karoo

ABSTRACT

Two new annual species of *Nemesia* Vent. are described from southern Africa. *Nemesia suaveolens* is characterized by magenta and yellow flowers. It differs from the closely related *N. euryceras* by having a lower lip that is yellow rather than white with pale violet margins, an upper lip with a conspicuous yellow rectangular patch just above the corolla opening, a spur that is $\pm$ equal to the length of the lower lip, not half the length, and a hypochile that is yellow rather than dark violet. This new species is known only from the arid Tanqua Karoo east of the Cedarberg Mountains. *N. aurantia* is characterized by orange saccate flowers with a brown and orange bearded palate. It is closest to *N. versicolor*, but differs from that species by its orange corolla, the absence of a spur, and its bearded palate with brown and orange trichomes. It is known from a single locality adjacent to the Swart Doring River in Namaqualand between Nuwerus and Garies.

INTRODUCTION

Nemesia Vent. is a genus of $\pm$ 62 species of annual and perennial herbs endemic to southern Africa (Steiner 1994). It is over a hundred years since the last revision of the genus (Hiern 1904) and many new species have come to light in the intervening years (Steiner 1989, 1994, 2006). A partial revision for species occurring chiefly in KwaZulu-Natal was published by Hilliard & Burt (1986), but most of the new species that remain to be described occur in the Cape Floristic Region and southern Namibia, where $\pm$ 75 % of the species occur. The purpose of this paper is to describe two new species from arid areas in the Northern Cape Province of South Africa. Descriptions are based primarily on living material collected in the field and maintained in cultivation.

Nemesia suaveolens K.E.Steiner, sp. nov., *N. euryceras* Schltr. proxima, sed differt lobo inferiore flavido nec blanco et violaceomarginato, hypochilo corolla aureo non atroviolaceo, macula rectangulari citrina conspicua basi labio superioro.

TYPE.—Northern Cape, 3219 (Wuppertal): Tanqua Karoo, 1.9 km N of entrance to Stompiesfontein (11.1 km N of Elandsvele turnoff), S32° 14.392' E19° 41.463', 330 m, (–BA), 1 Sept. 2007, Steiner 4286 (NBG, holo.; CAS, iso.).

Annual herb up to 320 mm tall, simple or branching from base; stems glandular pilose, rectangular in cross section, corners ridged, sides up to 1.8 mm wide, lateral stems up to 160 mm long. *Leaves* simple, opposite, mostly sessile to shortly petiolate; lamina lanceolate to ovate or elliptical, 4–22 $\times$ 2–12 mm, sparsely glandular pilose, apex rounded to acute; base rounded to cuneate; margins entire to shallowly and sparsely dentate; petioles 0–12 mm long, glandular pilose. *Flowers* axillary or in lax, terminal racemes, pleasantly spicy scented; racemes up to 270 mm long; bracts alternate, sessile,

cordate, reflexed, glandular pilose, lowermost leaf-like up to 12.5 $\times$ 8 mm, uppermost reduced to $\pm$ 3 $\times$ 3 mm, apex acute, base cordate; margins entire; pedicels 4–12 mm long, ascending, glandular pilose. *Calyx* lobes 5, lanceolate to ovate, acute, spreading, densely glandular pilose, central upper lobe lanceolate, 3.0–3.9 $\times$ 0.9–1.2 mm, upper lateral lobes lanceolate, 2.8–3.7 $\times$ 0.8–1.3 mm, lower lateral lobes ovate, 2.8–3.5 $\times$ 1.0–1.6 mm. *Corolla* bilabiate, 11.6–21.8 $\times$ 10.5–10.9 mm, upper lip 4-lobed, 2 inner lobes oblong to obovate, 6.4–6.7 $\times$ 2.6–3.1 mm, apices rounded to acute, bases strongly oblique, 2 outer lobes spreading to revolute, oblong, 3.1–5.1 $\times$ 3.2–4.1 mm, apices rounded to emarginate, bases strongly oblique; upper lip deep magenta at base (greyish magenta reverse) surrounding a bright golden yellow rectangular patch, 1.2–1.6 $\times$ 1.7–1.9 mm, just above corolla opening, becoming greyish white on lobes distally, lower lip widely obovate, 6.0–8.2 $\times$ 6–8 mm, apex emarginate, light yellow with yellowish white reverse, base with a raised palate; palate convex, oblong, cristate, 3.1–4.6 $\times$ 4.7–6.0 mm, divided by a central groove into 2 raised yellow bosses, bosses glabrous or with minute trichomes distally, densely pilose with conspicuous pale yellow or white trichomes basally around corolla opening; hypochile (floor of corolla tube) $\pm$ 3.9–4.1 mm long, central boss low, densely pilose, trichomes white to pale yellow; sides and upper inside surface of corolla tube greyish with magenta to purple lines, base of tube with a narrow spur, 3.5–4.8 $\times$ 0.7–0.8 mm, pale yellow to whitish, deflexed and $\pm$ straight or curving forward slightly in distal third, outside sparsely glandular pubescent, spur opening flanked by 2 greenish yellow to orange patches. *Stamens* 4, usually white, purple flecked distally, lying in a shallow depression (2.5–2.9 $\times$ 0.8–1.0 mm) in upper inside surface of corolla tube; filaments of antecus pair (twisted into posticus position) 2.7–2.8 mm long, sigmoid, $\pm$ straight in middle, glabrous or with a few glandular trichomes below middle; posticus filaments $\pm$ straight except at base, 0.8–1.0 mm long, glandular pubescent; anthers 0.9–1.0 mm long, each pair strongly coherent. *Ovary* oblong-ovoid, 1.2–1.6 $\times$ 1.0–1.6 mm, laterally compressed; style oblong, $\pm$ 0.8 mm long, compressed

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FIGURE 1.—*Nemesia suaveolens*, Steiner 4288 (CAS, NBG). A, habit; B, calyx. C–F, corolla: C, front view; D, side view; E, rear view; F, side view partially cut away. G, stamens, anticus left, posticus right; H, pistil; I, capsule; J, seed. Scale bars: A, 10 mm; B, 3 mm; C–F, 2 mm; G, H, 1 mm; I, 2.5 mm; J, 1 mm. Artists: A–H, John Manning; I, Sarah Adler; and J, Nicole Bollinger.

contrary to ovary, lying between anther pairs and curving slightly away from corolla opening; stigma crescent-shaped, 0.1×0.5 mm. *Capsules* ovate to oblong in outline, $3.9\text{--}10.6 \times 3.6\text{--}6.5$ mm, laterally compressed contrary to septum, apex emarginate to bilobed, lobes rounded. *Seeds* winged, ovate to widely ovate, $\pm 1.5 \times 1.0\text{--}1.5$ mm, light brown, verrucate, wing membranous with numerous parallel, brownish veins. *Flowering time*: (May–)July–September. Figures 1; 2A, B.

Diagnostic features: *Nemesia suaveolens* is easily recognized by its yellow and magenta flowers with a $\pm$ straight spur and a prominent yellow rectangular spot (nectar guide) at the base of the upper corolla lip. It is most closely related to *N. euryceras*, but differs from

that species by having a lower lip that is yellow rather than white with pale violet margins, an upper lip with a conspicuous yellow rectangular patch, just above the corolla opening, a spur that is $\pm$ equal to the length of the lower lip, not half the length of the lower lip, and a hypochile that is yellow rather than dark violet. Schlechter (1899) and Hiern (1904) describe the lower lip of *N. euryceras* as sulphur yellow, but this is apparently based on a single flower on the type specimen (Schlechter 8126 at K) that became yellowish from drying. The other flowers on the same plant do not look yellowish, but rather are consistent with the author's observation at the type locality (Steiner 3686 at NBG) of a lower lip that is white with pale violet margins. Other collections in PRE from the type locality and nearby areas also give

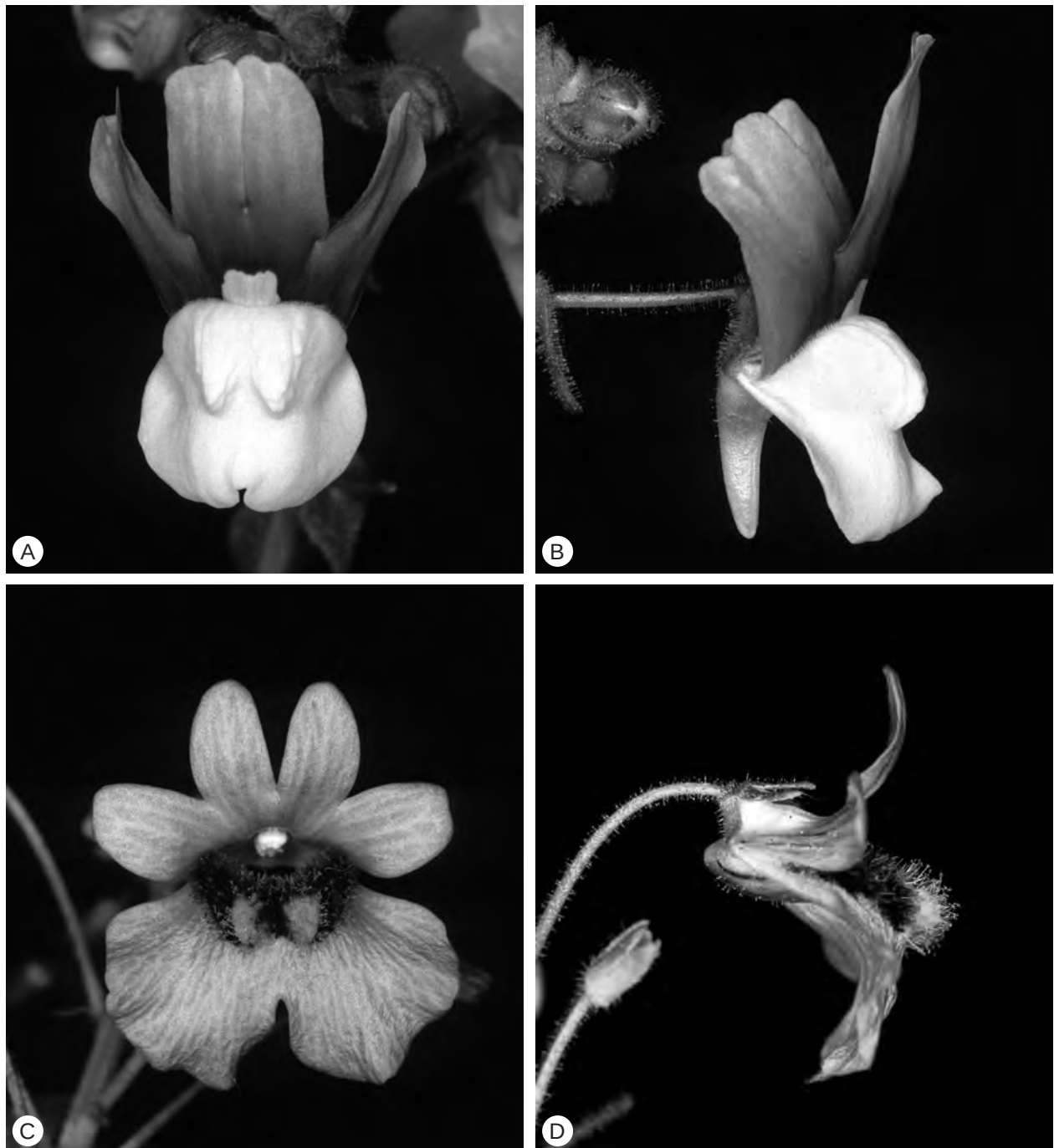


FIGURE 2.—*Nemesia* flowers: A, B, *N. suaveolens*: front and side views; C, D, *N. aurantia*: front and side views.

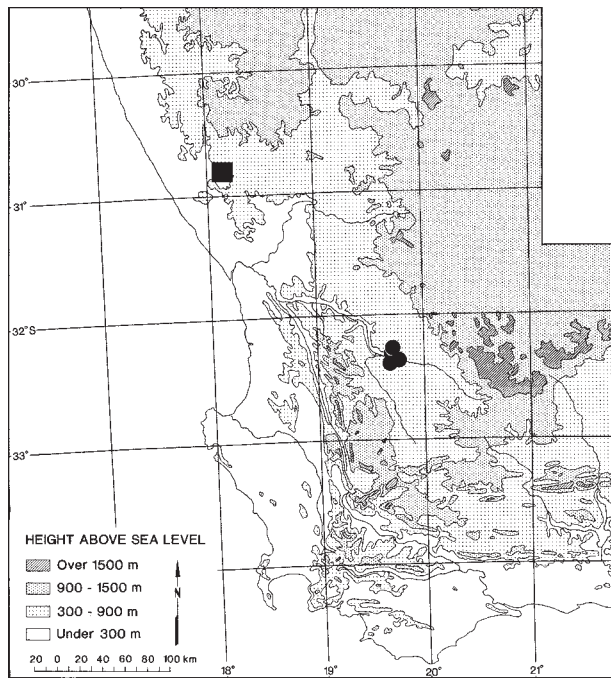


FIGURE 3.—Known distribution of *N. suaveolens*, ●; and *N. aurantia*, ■.

flower colour as white and purple, mauve and white, or pink (e.g. *Grant 4763*; *Hall 3726*; *Le Roux 2167*).

Nemesia suaveolens often grows in close proximity to *N. karroensis* Bond and has been confused with that species. It is similar in coloration to *N. karroensis*, especially when both are pressed and dried, but differs in having a short, straight, downwardly oriented spur instead of a long (8.9–12.3 mm), backwardly projecting one that is usually strongly recurved in its distal half (Bond 1940).

Etymology: the name refers to the pleasant spicy fragrance of the flowers.

Distribution and habitat: *Nemesia suaveolens* is known from a very limited area of the central Tanqua Karoo at elevations between 320 and 445 m (Figure 3). The Tanqua is an arid desert plain situated in the rain shadow of the Cedarberg Mountains that receives only 50 to 70 mm of rainfall in an average year, mostly falling in late autumn or early winter. *N. suaveolens* is an annual that germinates in response to these rains, but in years of no appreciable rainfall, plants remain dormant as seeds.

Breeding systems: in cultivation, where insects are excluded, *Nemesia suaveolens* does not set seed. This suggests that, like many *Nemesia* species, this species is self-incompatible. Although pollinators were not encountered on flowers in the field, the presence of capsules suggests that plants were successfully pollinated. The spurs of *N. suaveolens* do not secrete nectar, so pollinating insects only obtain pollen as a reward.

Other specimens examined

NORTHERN CAPE.—3219 (Wuppertal): Tanqua Karoo, Ceres–Calvinia road (R355), 13.4 km N of turnoff to Elandsvlei, S32° 13.487' E19° 42.086', ± 320 m, (–BA), 23 Aug. 2004, *Steiner 4069* (CAS);

Tanqua Karoo, 13.4 km N of Elandsvlei turnoff (4.2 km N of entrance to Stompiesfontein), S32° 13.279' E19° 42.195', 324 m, (–BA), *Steiner 4288* (CAS, NBG); Tanqua Karoo, Ceres–Calvinia road (R355), 13.9 km N of turnoff to Elandsvlei, S32° 13.311' E19° 42.189', ± 320 m, (–BA), 23 Aug. 2004, *Steiner 4070* (CAS); Tanqua Karoo, Stompiesfontein, (–BA), 26 July 1941, *Bond 1181* (NBG); Tanqua National Park, Bo Stompiesfontein and Varsfontein, S32° 12' 56" E19° 43' 02.1", 368 m, (–BA), 25 July 2006, *Rosch 415* (NBG); 4.8 km NNE of Kommando Drift, ± 375 m, (–BC), 30 Aug. 1957, *Acocks 19477* (PRE); near Eendjies Kraal [Uintjieskraal] on road to Hottentots Kloof, (–BD), 28 Sept. 1929, *Grant 4909* (PRE); Tanqua Karoo, 6.1 km S of Papkuil on Ceres–Calvinia road, [± 442 m], (–DA), 17 May 1983, *Snijman 1274* (NBG); Coega Kamma, 70 miles [112 km] from Ceres (–DA), 25 Aug. 1968, *Stayner s.n.* (NBG). 3220 (Sutherland): south of Tanqua National Park on Middlepos–Ceres road, after Platfontein turnoff, Farm No. 10, 390 m, (–AC), 11 July 2006, *Rosch 353* (NBG).

***Nemesia aurantia* K.E.Steiner, sp. nov., *N. versicolori* Drège proxima, sed differt floribus aurantis, corolla saccato, non calcarato, palato barbato brunneo et aurantio.**

TYPE.—Northern Cape, 3018 (Kamiesberg): Farm Stinkfontein, ± 160 m, (–CC), 20 Aug. 2001, *Steiner 3640* (NBG, holo.; CAS, iso.).

Annual herb up to 410 mm tall, simple or branching; stems glandular pilose, rectangular in cross section, corners ridged, sides up to 2 mm wide, lateral stems up to 265 mm long. *Leaves* simple, opposite, glabrous, apices acute, bases cuneate to truncate, margins sparsely dentate; basal leaves ovate to elliptical, 10.8–18.4 × 3.1–8.4 mm; petioles up to 7 mm long; upper leaves sessile, lanceolate to linear, 9.0–39.6 × 1.3–9.4 mm, glabrous. *Inflorescence* terminal, racemose, up to 190 mm long, or flowers axillary; bracts alternate, sessile, reflexed, narrowly lanceolate to deltoid, 1.1–2.4 × 0.9 mm, glabrous above, sparsely glandular puberulent below, apex acute, base truncate; margins entire; pedicels ± 8–24 mm long, ascending, glandular pilose. *Calyx* lobes 5, spreading, acute, densely glandular pilose, upper and lateral lobes oblong, ± 2.5 × 0.8 mm, lower lobes shorter, lanceolate, ± 2.1 × 0.8 mm. *Corolla* bilabiate, 13.1–18.8 × 11.1–16.0 mm, upper lip 4-lobed, 2 inner lobes oblong to obovate, 5.1–6.2 × 1.9–3.2 mm, apices rounded to acute, bases strongly oblique, 2 outer lobes spreading, oblong, 4.7–6.5 × 3.4–4.1 mm, apices emarginate, bases strongly oblique; all lobes orange distally and pale yellow with brownish streaks at base, lower lip widely obcordate, 9.2–12.3 × 10.5–16.0 mm, deep orange, basal portion inflated into a dark brown, convex palate, 4.1–8.0 × 4.5–5.2 mm long; bosses 2, oblong, divergent, orange, 0.5–1.7 × 1.3–1.4 mm, densely villous, trichome stalks pale yellow or brown, translucent, simple or branched below head, heads capitate or discoid; hypochile (floor of corolla tube) ± 3.7–4.1 × 4 mm, ± flat, streaked with reddish brown, sparsely to densely pilose, especially on inner lateral walls, outer surface glandular pilose; upper inside surface of corolla tube pale yellow with brown lines, base shallowly saccate, 0.7–1.0 × 4.7–4.9 mm, pale yellow, lower outside portion pilose. *Stamens* 4, lying in a shallow depression in upper inside surface of corolla tube; filaments of anticus pair (twisted into posticus position) ± 2.2 mm long, sigmoid, ± straight in middle, glabrous; posticus filaments ± 1.5 mm long, straight except at base, glabrous; anthers ± 1.1–1.2 mm long, each pair strongly coherent, opening downward. *Ovary* oblong-ovoid, ± 1.0–1.2 × 0.9–1.0 mm, later-

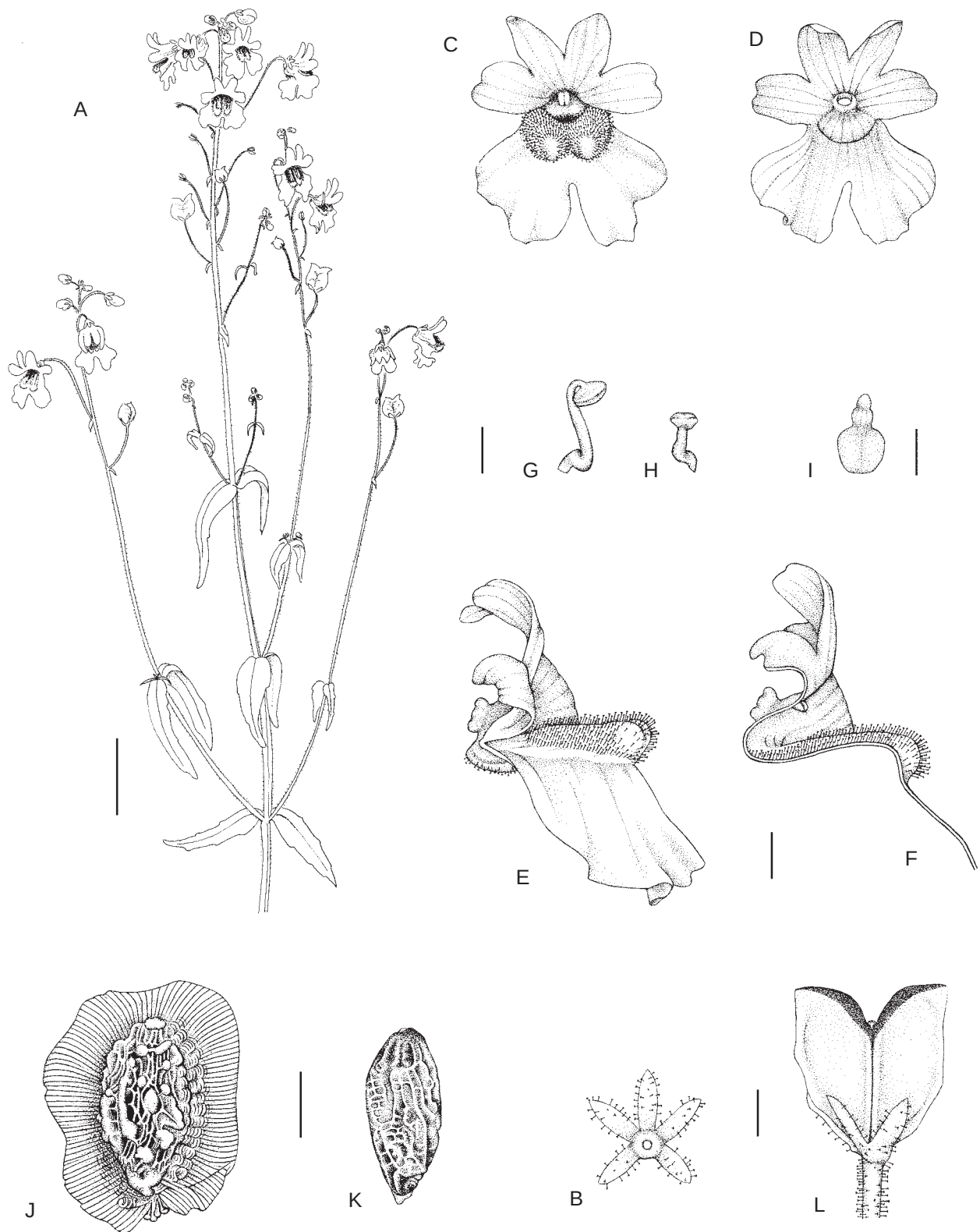


FIGURE 4.—*Nemesia aurantia*, Steiner 3640 (CAS, NBG). A, habit; B, calyx. C–F, corolla views: C, front, D, rear; E, corolla intact; F, corolla partially cut away. G, H, stamens: G, anticous, H, posticous. I, pistil. J, K, seed: K, with outer coat and wing removed. L, mature capsule. Scale bars: A, 20 mm; B, E, F, L, 2 mm; C, D, 5 mm; G, H, J, K, 0.5 mm; I, 1 mm. Artists: A, Inge Oliver[†]; C–K, Nicole Bollinger.

ally compressed; style ± 0.5 mm, deflected away from corolla opening, oblong, truncate, lying between anther pairs; stigma deltoid $\pm 0.3 \times 0.5$ mm. *Capsules* ovate to oblong in outline, $\pm 3.8\text{--}8.3 \times 4.5\text{--}7.0$ mm, compressed contrary to septum, apex emarginate to bilobed, lobes acute to rounded. *Seeds* winged, ovate to widely

ovate, $1.7\text{--}2.4 \times 1.3\text{--}2.1$ mm, outer layer of testa white, lacey, verruculate, enveloping inner seed at maturity, wing membranous with numerous parallel white veins, internal portion of seed narrowly elliptical, dark brown, $1.0\text{--}1.2$ mm long, surface alveolate. *Flowering time*: August–September. Figures 2C, D; 4.

Diagnostic features: *Nemesia aurantia* is most closely related to *N. versicolor*, but has orange rather than blue or yellow flowers, lacks a conspicuous spur, and has a bilobed palate on the lower lip that is less prominent. The only other saccate *Nemesia* species with orange flowers is *N. strumosa* Benth. Plants of *N. aurantia* are typically shorter than *N. strumosa* (up to 410 mm vs up to 730 mm) with smaller flowers (corolla limb 13–19 mm vs 17–35 mm long). The sac of the corolla in *N. aurantia* is less than half the length, on average, of *N. strumosa* and the raised palate and divergent bosses on the lower lip of *N. aurantia* are absent in *N. strumosa*.

Etymology: the name refers to the bright orange flowers.

Distribution and habitat: *Nemesia aurantia* is known only from the Northern Cape, just north of its boundary with the Western Cape, ± 31 km S of Garies. It occurs with *Arctotis fastuosa* in a very localized area of loose sand near the Swart Doring River on the Farm Stinkfontein (Figure 2).

Conservation status: until other populations have been located, this species should be considered rare. The intensity of sheep grazing on the Farm Stinkfontein is currently unknown, but may represent a threat to the long-term survival of this population.

Pollination and breeding systems: nothing is known about the pollination biology of *Nemesia aurantia*, but because of its open saccate flowers, bright orange colour, and densely pubescent palate, it may be pollinated by small monkey beetles. Based on the absence of capsule formation in cultivation, *N. aurantia* is probably self-incompatible.

Other specimens examined

NORTHERN CAPE.—3018 (Kamiesberg): Farm Stinkfontein, 950 feet [± 300 m], (–CC), 21 Sept. 1929, *Grant & Theiler 4778* (BOL, K). Locality uncertain: Namaqualand, along road, Garies to O’Okiep, Aug. 1925, *Marloth 6742* (NBG).

ACKNOWLEDGEMENTS

I thank Northern and Western Cape Nature Conservation authorities for permission to collect in their respective areas. I also thank John Manning, Inge Oliver[†], Nicole Bolinger, and Sarah Adler for their contributions to the illustrations. I am grateful to Dee Snijman and the Compton Herbarium staff for help with localities and for the use of their facilities. I also thank SANBI for *Nemesia* loans from NBG and PRE.

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Taxonomy and phylogeny of two subgroups of *Pelargonium* section *Otidia* (Geraniaceae). 1. The *Pelargonium carnosum* complex

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Keywords: amplified fragment length polymorphism (AFLP), distribution, Geraniaceae, hybridization, morphology, *Pelargonium carnosum* (L.) L'Hér., phylogeny, South Africa, taxonomy, winter rainfall area

ABSTRACT

This contribution deals with the taxonomy and phylogeny of the *Pelargonium carnosum* complex, a group of closely related taxa of *Pelargonium* L'Hér. section *Otidia* (Sweet) DC. (Geraniaceae) that is distributed in the winter rainfall area of South Africa. According to molecular analyses via AFLP, *P. adriaanii* M.Becker & F.Albers, *P. carnosum* (L.) L'Hér., *P. ferulaceum* (Cav.) Willd. and *P. polycephalum* (E.Mey. ex Harv.) R.Knuth form a monophyletic clade. Although hybridization may occur between the taxa, three are assigned to specific rank. The fourth taxon, *P. ferulaceum* is recognized as a subspecies of *P. carnosum*. As is implied from the occurrence of morphological intermediates and partly from molecular evidence, hybridization does not only occur among the taxa in this complex but also involves species closely related to this group (*P. parviflorum* J.C.Wendl., *P. laxum* (Sweet) G.Don, *P. dasyphyllum* R.Knuth). For the taxa in the *P. carnosum* complex, distribution areas are delineated and diagnostic features that have until now remained obscure, are outlined.

INTRODUCTION

The genus *Pelargonium* L'Hér. comprises $\pm$ 280–290 species which are subdivided into 16 sections (Bakker *et al.* 2004). The infrageneric classification relies on molecular evidence, on differences in chromosome sizes and basic chromosome numbers, and on geographical distribution and growth forms. Within the major group characterized by small chromosomes, section *Otidia* (Sweet) DC. belongs to a subgroup showing xerophytic growth. Within this 'xerophytic clade', it is part of the so-called winter rainfall clade (Bakker *et al.* 2004). Section *Otidia* comprises 25 taxa, some of them distinctive and isolated, others closely related and hardly distinguishable.

The *Pelargonium carnosum* (L.) L'Hér. complex includes several taxa that are linked by intermediates. Morphological intermediates are usually assigned to introgression. The close relationship of these taxa was recognized early in the taxonomic history of *Pelargonium*. Harvey (1860), when describing *P. polycephalum* (E.Mey. ex Harv.) R.Knuth as *P. ferulaceum* var. *polycephalum*, stressed its strong resemblance to *P. carnosum*. Dyer (1953) reduced *P. ferulaceum* (Cav.) Willd. and *P. polycephalum* to the rank of a variety under *P. carnosum*, which can be taken as the year of inception of the *P. carnosum* complex. Becker & Albers (2005a) added *P. adriaanii* M.Becker & F.Albers, thus increasing the number of taxa in this complex to four: *P. adriaanii*, *P. carnosum*, *P. ferulaceum* and *P. polycephalum*.

Vorster (1990) placed the closely related *Pelargonium parviflorum* J.C.Wendl. in the *P. carnosum* complex as well. However, as *P. parviflorum* comprises several taxa that are characterized by a distinctive floral structure, we prefer to treat it as a separate taxon and with further taxa as a separate subgroup (*P. parviflorum* complex, Becker & Albers in press a).

A phylogenetic tree that results from extensive molecular analyses is presented. Polymorphic markers have been detected via AFLP (amplified fragment length polymorphism, Vos *et al.* 1995), a method that requires no previous knowledge of DNA sequences and provides a large amount of reliable and repeatable bands. AFLP markers are generated from the entire spectrum of genomic DNA including fast evolving regions, leading to a high resolution at the subspecies and even population level in phylogenetic analyses. We discarded sequence analyses based on nuclear ITS and plastid *trnL*-*trnF* regions, as the differences between studied taxa were too marginal.

MATERIAL AND METHODS

Plant material

Specimens of the living collection of Münster Botanical Garden (Table 1) were included in the molecular analysis. Voucher specimens were deposited in MSUN. For delimiting the distribution ranges of the taxa, 224 herbarium specimens were examined from the following herbaria: BM, BOL, K, MSUN, NBG and PRE—acronyms as in Holmgren *et al.* (1990).

DNA extraction and AFLP analysis

Genomic DNA was extracted from $\pm$ 500 mg of fresh leaf tissue per plant following the CTAB procedure described by Doyle & Doyle (1987) and modified by Bakker *et al.* (1998). AFLP (amplified fragment length polymorphism) analyses were performed using the protocol of Vos *et al.* (1995), with minor modifications (Marschalek 2003). DNA was restricted with enzymes EcoRI (rarely cutting) and MseI (frequently cutting). Single strands of EcoRI and MseI adapter were 3'-CATCTGACGCATGGTTAA-5', 5'-CTCGTAGACTGCGTACC-3' and 3'-TACTCAGGACTCAT-5', 5'-GACGATGAGTCCTGAG-3', respectively. Nine combinations of primers based on three selective bases (EcoRI-AAC, -AGG, -ATA and MseI -CAA, -CAG, -CCG, -CGA,

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MS. received: 2007-05-30.

TABLE 1.—Localities, collectors' names and numbers of specimens in *Pelargonium carnosum* complex and further species of sect. *Otidia* from South Africa (RSA) and Namibia selected for AFLP analyses. Grid references given per quarter-degree square. STEU = Stellenbosch University Botanical Garden

Taxon	Grid ref.	Locality	Collector	Coll. no.
Sect. <i>Otidia</i> s.l.				
<i>P. alternans</i>	3218 BB	Pakhuispass (RSA)	Boucher	STEU 974
<i>P. ceratophyllum</i>	2615 CA	Lüderitz (Namibia)	Albers & Becker	4212
<i>P. crithmifolium</i>	3017 AD	Wallekraal (RSA)	Albers & Becker	4345
<i>P. dasyphyllum</i>	2917 DB	Steinkopf (RSA)	Albers & Becker	4291
<i>P. klinghardtense</i>	2816 DA	Beauvallon (RSA)	Albers & Becker	4249
<i>P. paniculatum</i>	2816 BB	Richtersveld (RSA)	Albers & Becker	4242
<i>P. laxum</i>	3325 DC	Redhouse (RSA)	Van der Walt	568
<i>P. parviflorum</i> complex				
<i>P. parviflorum</i>				
subsp. <i>karasbergense</i>	2718 CA	Klein Karas (Namibia)	Albers & Becker	4188
subsp. <i>parviflorum</i>	2917 BB	Steinkopf (RSA)	Albers & Becker	4229
subsp. <i>rotundipetalum</i>	3320 DC	Muiskraal (RSA)	Albers & Meve	125
subsp. <i>tuberculum</i>	2716 DA	Rosh Pinah (Namibia)	Albers & Becker	4205
<i>P. parviflorum</i> s.l.	3017 BB	Kamieskroon (RSA)	Albers & Becker	4348
<i>P. brevipetalum</i>	3320 BA	Matjiesfontein (RSA)	Albers & Becker	4462
<i>P. carnosum</i> × <i>P. parviflorum</i>	3218 BB	Clanwilliam (RSA)	Albers & Becker	4405
<i>P. carnosum</i> complex				
<i>P. adriaanii</i>	2916 BB	Port Nolloth (RSA)	Albers & Becker	4236
	2916 BB	Port Nolloth (RSA)	Albers & Becker	4237
	2916 BB	Port Nolloth (RSA)	Albers & Becker	4238
<i>P. carnosum</i> subsp. <i>carnosum</i>	3217 DB	Stompneus Bay (RSA)	Albers & Becker	4419
	3318 AA	Langebaan (RSA)	Albers & Becker	4430
	3318 AC	Yzerfontein (RSA)	Van der Walt	STEU 1815
<i>P. carnosum</i> subsp. <i>ferulaceum</i>	3319 BB	Karoopoort (RSA)	Albers & Becker	4118
	3319 BB	Karoopoort (RSA)	Albers & Becker	4120
	3319 CB	Worcester (RSA)	Albers & Becker	4435
<i>P. polycepalum</i>	2917 BB	Steinkopf (RSA)	Albers & Becker	4232
	2917 BB	Steinkopf (RSA)	Albers & Becker	4313
	2917 DB	Goegap NP (RSA)	Albers & Becker	4298
Hybrid 1	3118 DA	Vredendal (RSA)	Albers & Becker	4373
	3217 DD	Paternoster (RSA)	Albers & Becker	4426
	3318 BD	Malmesbury (RSA)	Van der Walt	STEU 2401
	3320 DC	Barrydale (RSA)	Albers & Becker	4444
Hybrid 2	3118 CA	Papendorf (RSA)	Albers & Becker	4389
	3118 CC	Doringbaai (RSA)	Albers & Becker	4397

-CTA) were chosen for the second selective PCR amplification. EcoRI primer was fluorescence labeled (IRDye™ 800 infrared dye, Licor). Electrophoresis of AFLP fragments was done on 7 % (w/w) polyacrylamide gels (250 × 0.2 mm) on a one-dye model 4200 Licor DNA automatic sequencer.

Cladistic analysis

Each AFLP fragment was counted as a separate putative locus and scored as present (1) or absent (0) for each sample. Only polymorphic bands that could be read unambiguously on each gel image were used for data analysis.

Phylogenetic analyses were performed with PAUP Version 4.0b10 (Swofford 2002), using *neighbour joining* (NJ; Restriction-site distances: Upholt) and a *maximum parsimony* criterion. For the latter, starting trees were generated by stepwise addition, swapping on best tree only in case of multiple trees. One thousand random addition replicates were chosen. The heuristic search

for best topologies used TBR branch swapping. Support for clades in both distance and parsimony analyses was measured using the non-parametric bootstrap method (Felsenstein 1985; 10 000 replicates).

RESULTS

The taxa in the P. carnosum complex: etymology and taxonomic history

The oldest mention of *Pelargonium carnosum* is found on a herbarium sheet dating back to 1724 (BM649367, Figure 1A). The brief diagnosis reads: '*Geranium africanum frutescens, Chelidonii folio; petalis florum angustis, albidis; carnosum caudice*'. The herbarium specimen originates from a plant that arrived at Chelsea Physic Garden in London in the same year. The collector and place of origin of this specimen are not known. A first detailed description of *P. carnosum* was provided by Dillenius in 1732, who described the species under the phrase name '*Geranium Afric. carnosum, petalis angustis albicantibus*'—a pre-Lin-

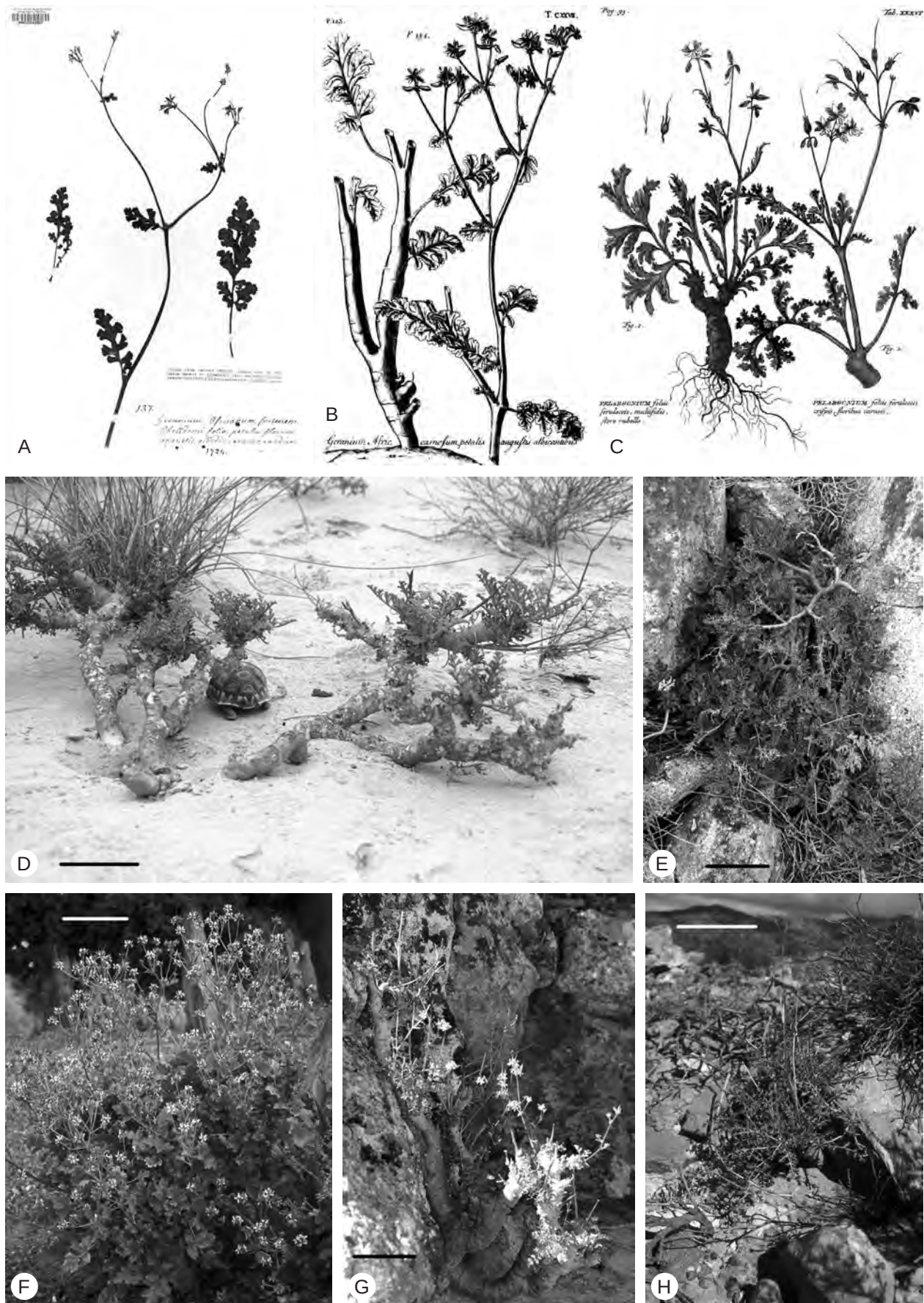


FIGURE 1.—A, B, *Pelargonium carnosum* subsp. *carnosum*, BM649367: A, one of the earliest herbarium specimens; B, lectotype; C, lectotype of *P. carnosum* subsp. *ferulaceum*. D–H, habit: D, *P. adriaanii*; E, *P. carnosum* subsp. *carnosum*; F, G, *P. polycepalum*; H, *P. carnosum* subsp. *ferulaceum*. D, E, G, H, plant's natural setting; F, in Worcester Botanical Garden. Scale bars: 100 mm.

nean name not valid according to the rules of the International Code of Botanical Nomenclature (ICBN). Although Dillenius did not give any indication as to the origin of the material examined by him, it can be assumed from the wording of the phrase name that he had indeed seen that particular herbarium specimen from 1724. In 1755 the species became the first member of (the later) section *Otidia* to be described by Linnaeus which he placed under the genus *Geranium* as *G. carnosum*, as he did not distinguish the genus *Pelargonium*. Linnaeus referred to Dillenius's illustration as the iconotype that accompanied the phrase name of *Geranium carnosum* (Figure 1B). Linnaeus's specific epithet, *carnosus*, the Latin word for fleshy or succulent, refers to the succulent stem as a presumed characteristic feature—but nonetheless fairly common within section *Otidia*—which he chose to separate *P. carnosum* from *P. gibbosum* (sect. *Polyactium*, with swollen nodes of the stem). In 1789, L'Héritier placed the species under *Pelargonium*.

The first diagnosis of *Pelargonium ferulaceum* was published by J. Burman in 1738 under the phrase name '*Pelargonium foliis ferulaceis, multifidis, flore rubello*'. The first part of the description refers to the deeply incised delicate leaves that resemble those of the genus *Ferula* (Apiaceae). The illustration by Burman is regarded as the iconotype. Burman's son (1759) was the first to adopt the Linnaean binary nomenclature and, hence, has traditionally been accepted as the author of this species name. Though he referred to his father's illustration (Figure 1C), he obviously described a member of section *Polyactium*: 'dwarf plant lacking stems, a simple stalk rising from the centre of the root-bearing long-tubed flowers as found in *Geranium triste*'. Due to this error, we propose to drop Burman filius as author of *P. ferulaceum*. Instead, Cavanilles (1787) should be credited as the author who took up a part of J. Burman's diagnosis when describing '*Geranium ferulaceum*'. Willdenow (1800) placed this species under the genus *Pelargonium*.

Pelargonium polycephalum was introduced by Meyer (1843) who referred to the numerous capitate pseudo-umbels as the character of distinction in this species (*poly* is the Greek word for many, and *cephalum* is the Greek word for head). As Meyer failed to publish a proper diagnosis, Harvey (1860) is credited as author of this species' name. A specimen collected by Drège was designated as the holotype. Harvey described the species under the name *P. ferulaceum* var. *polycephalum* with *P. carnosum* as the most closely related taxon. In 1912 Knuth raised the taxon to specific rank as *P. polycephalum*.

The last species described in this complex was *Pelargonium adriaanii* M.Becker & F.Albers which was published by the present authors in 2005 in honour of the late J.J. Adriaan van der Walt for his valuable contributions in the genus.

Key to taxa

- 1a Pedicel longer than hypanthium *P. adriaanii*
- 1b Pedicel shorter than hypanthium:
 - 2a Compact pseudo-umbel with $\pm$ 10 flowers *P. polycephalum*
 - 2b Loose pseudo-umbel with 4–6 flowers:
 - 3a Leaves pinnately incised. *P. carnosum* subsp. *carnosum*
 - 3b Leaves bipinnately divided, pinnae petiolate *P. carnosum* subsp. *ferulaceum*

Pelargonium carnosum and *P. ferulaceum* are treated as subspecies, due to their close relationship and the frequent occurrence of hybrids (see below). With *P. carnosum* being the older name of the two, the correct names are *P. carnosum* subsp. *carnosum* and *P. carnosum* subsp. *ferulaceum* (Cav.) M.Becker & F.Albers, comb. nov. *Pelargonium adriaanii* and *P. polycephalum* are still treated as separate species.

1. ***Pelargonium adriaanii*** M.Becker & F.Albers in *Botanische Jahrbücher* 126,2: 153 (2005a). Type: Northern Cape, 2916 (Port Nolloth), (–BB), 17 Sept 2003, Becker & Albers 4235 (MSUN, holo.!).

2a. ***Pelargonium carnosum*** (L.) L'Hér. in Aiton, *Hortus kewensis* 2: 421 (1789). *Geranium carnosum* L.: 20 (1755). *Otidia carnosa* (L.) Sweet: t. 98 (1822). *Geranospermum carnosum* (L.) Kuntze: 94 (1891). Lectotype: *Geranium africanum carnosum* Dill.: 153, t. 127, fig. 154 (1732).

Pelargonium sisonifolium Baker, t. 28 (1869). Lectotype: 'Cape' [icono., Baker in Saunders, *Refugium Botanicum*: t. 28 (1869)].

2b. ***Pelargonium carnosum*** subsp. ***ferulaceum*** (Cav.) M.Becker & F.Albers, comb. nov.

Geranium ferulaceum Cav., *Quarta Dissertatio botanica*: 265, t. 110, fig. 2 (1787). *Pelargonium ferulaceum* (Cav.) Willd.: 687 (1800). *Otidia ferulacea* (Cav.) Eckl. & Zeyh.: 69 (1835–1837). *Geranospermum ferulaceum* (Cav.) Kuntze: 94 (1891). Lectotype: *Pelargonium foliis ferulaceis* Burm.: 93, t. 36, fig. 1 (1738).

Pelargonium mammulosum J.C.Wendl.: 77 (1810). *Otidia burmaniana* Eckl. & Zeyh., non DC.: 69 (1835–1837). *Pelargonium burmanianum* Steud.: 284 (1841). Lectotype: 'Vorgebirge der guten Hoffnung' [icono., Wendl., *Collectio plantarum* 2: t. 70 (1810)].

3. ***Pelargonium polycephalum*** (Harv.) R.Knuth ex E.Mey. in Drège, *Zwei pflanzengeographische Dokumente*: 209 (1843–1844); Engler: 372 (1912). *P. ferulaceum* var. *polycephalum* Harv.: 279 (1859–1860). Type: Northern Cape, 'Kous–Silverfontein', Drège 3244 (according to Knuth 1912), *nomen nudum* by E. Meyer: 209 (1843–1844).

Morphological characters of section *Otidia*

In addition to the commonly occurring succulent stems and pinnate leaves, the set of characters defining section *Otidia* also includes short-spurred flowers.

The typical auricles borne at the base of the posterior petals are restricted to this section, although similar petal structures are found in certain species of sections *Campylia*, *Hoarea*, *Ligularia* and *Pelargonium* (Struck 1997). Stamens that curl upwards at the end of the staminate phase are restricted to section *Otidia* and a couple of species in section *Pelargonium* (Struck 1997).

Pelargonium alternans J.C.Wendl. which hitherto has also been placed in section *Otidia*, differs in various characters (Becker & Albers in press b). A large genetic gap between this species and the rest of the section has been established (Bakker *et al.* 2004; Becker & Albers in press c), and *P. alternans* is excluded from the section in the strict sense (= *Otidia s.str.*) in the present account. We refer to *Otidia s.l.* in order to indicate traditional circumscription of the section, i.e. including *P. alternans*.

The taxa in the *Pelargonium carnosum* complex do not differ much from the other members of section *Otidia*. However, most taxa in the *P. carnosum* complex and the closely related *P. parviflorum* complex (Becker & Albers in press a) are distinguished by a character which is otherwise absent in the section (except in *P. alternans*): the pedicel is much shorter than in the remaining *Otidia* species. The ratio between the lengths of hypanthium and pedicel—a valuable characteristic in *Pelargonium* (Miller 1996)—varies between 2 and 10 within both complexes, but between 0.1 and 1.0 in the remaining members of *Otidia* s.str. However, *P. adriaanii* does not fit into this pattern: in this species the pedicel is much longer than the hypanthium. Therefore, no phenotypic character clearly delineates the *P. carnosum* complex. The taxa in the *P. parviflorum* complex differ from those in the *P. carnosum* complex in possessing tiny, mostly yellowish petals.

Diagnostic features in the *P. carnosum* complex (Table 2)

Pelargonium adriaanii (Figure 1D) and *P. polycephalum* (Figure 1F, G) can develop into large plants of 1 m across that possess stems of 50 mm in diameter. In *P. carnosum* subsp. *carnosum* (Figure 1E) the stems are much thinner and in subsp. *ferulaceum* (Figure 1H) they remain shorter.

In *Pelargonium adriaanii* and *P. carnosum* subsp. *carnosum* the lateral roots form series of small tubers; *P. carnosum* subsp. *ferulaceum* and *P. polycephalum* exhibit a simple root system without any thickenings.

Apart from their pinnate shape, the leaves do not share a further character. They differ in the degree of succulence and density of the indumentum (Figure 2A). In *Pelargonium carnosum* subsp. *carnosum* and *P. adriaanii*, the leaves are rather herbaceous and densely covered with partially very long hairs; in *P. carnosum* subsp. *ferulaceum* and *P. polycephalum*, the leaves are slightly succulent and covered with microscopical papillae. Conversely, Harvey in his description of *P. polycephalum*, maintained that the leaves are much more hairy in this species than in *P. carnosum* s.str., although the reverse is correct according to our observations. Leaf shapes differ clearly in the four taxa: in *P. carnosum* subsp. *carnosum* and *P. polycephalum*,

the leaves are mostly pinnately incised, but bipinnately divided in *P. carnosum* subsp. *ferulaceum* and in *P. adriaanii*. In *P. carnosum* subsp. *ferulaceum* almost all pinnae have a petiolule, but only the first pair of pinnae in the remaining three taxa have a petiolule. Petioles tend to persist in section *Otidia* and old leaf bases cover the stems as acute or blunt, ‘thorny’ fragments. Only in *P. carnosum* subsp. *carnosum* are the petioles usually shed with the rest of the leaves, giving the stems a smooth overall outline.

As to floral structure, the four taxa in the complex can be divided into two groups: 1, *Pelargonium adriaanii*; and 2, *P. carnosum* subsp. *carnosum*, *P. carnosum* subsp. *ferulaceum* and *P. polycephalum*. The pedicel is exceptionally long in *P. adriaanii* (Figure 2F) compared to those of all other taxa in the *P. carnosum* complex and the pseudo-umbels of the first taxon appear fairly loose. In contrast, the pseudo-umbels of *P. carnosum* subsp. *carnosum* (Figure 2B), *P. carnosum* subsp. *ferulaceum* (Figure 2C, E) and *P. polycephalum* (Figure 2G) appear rather compact due to the very short pedicels. The capitate shape of the pseudo-umbels in *P. polycephalum* results from the shortened hypanthia and a higher number of flowers per partial inflorescence. *P. carnosum* subsp. *carnosum*, *P. carnosum* subsp. *ferulaceum* and *P. polycephalum* exhibit long and narrow petals. The flowers are most commonly white in all three taxa sometimes suffused with pink and bearing dark pink markings or stripes on all five petals (Figure 2D, E). Since there is no detectable pattern in the distribution of these variations in floral pigmentation, the three taxa can be separated as a subgroup with respect to flower structure. Conversely, *P. adriaanii* exhibits the longest and broadest petals within section *Otidia* (Figure 2F). With the exception of their purple markings, the petals are pure white; no additional flower colour occurs.

A comparison of early and later states of inflorescence development reveals important distinctions (Figure 3). *Pelargonium carnosum* subsp. *carnosum* and *P. adriaanii* exhibit a loosely branched inflorescence with 4–5 nodes and each node generates a single or a branched peduncle (simplified in Figure 3). Altogether the inflorescence is composed of 6–12 pseudo-umbels with 4–6

TABLE 2.—Morphological differences in taxa of *Pelargonium carnosum* complex

	<i>P. adriaanii</i>	<i>P. carnosum</i>		<i>P. polycephalum</i>
		subsp. <i>carnosum</i>	subsp. <i>ferulaceum</i>	
Root swellings	+	+	-	-
Stem				
length	500–700 mm	500–700 mm	100–200 mm	500–700 mm
diameter	50 mm	30 mm	50 mm	50 mm
Leaf				
succulence	-	-	+/-	+/-
hairiness	+	+	-	-
pinnation	double	single	double	single
Pseudo-umbels per inflorescence	6–12	6–12	up to 50	up to 50
Flowers per pseudo-umbel	4–6	4–6	4–6	10–15
Pedicel length	20 mm	1–2 mm	1–2 mm	1–2 mm
Hypanthium length	5–7 mm	8–9 mm	8–9 mm	3–4 mm
Petal width	6–7 mm	3–4 mm	3–4 mm	3–4 mm

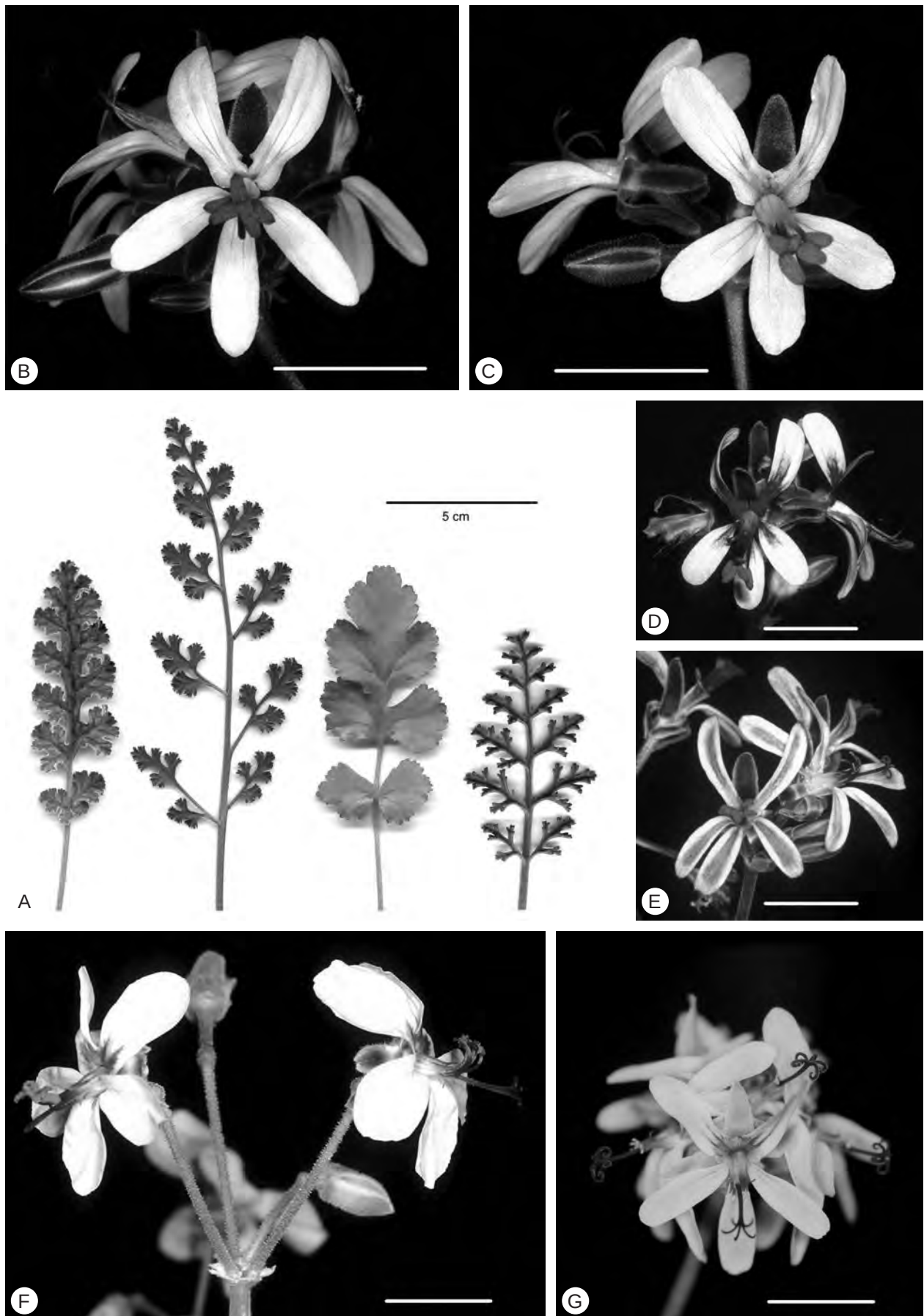


FIGURE 2.—Leaves and flowers of taxa in *Pelargonium carnosum* complex. A, leaves, from left to right: *P. carnosum* subsp. *carnosum* (STEU1815), *P. carnosum* subsp. *ferulaceum* (A&B4118), *P. polycephalum* (A&B4232), *P. adriaanii* (A&B4237). B–G, flowers: B, *P. carnosum* subsp. *carnosum* (STEU1815); D, *P. carnosum* subsp. *carnosum* × *P. carnosum* subsp. *ferulaceum* (A2622). C, E, *P. carnosum* subsp. *ferulaceum*: C, (A&B4118); E, (A&B4435). F, *P. adriaanii* (A&B4237); G, *P. polycephalum* (A&B4232). Scale bars: 10 mm.

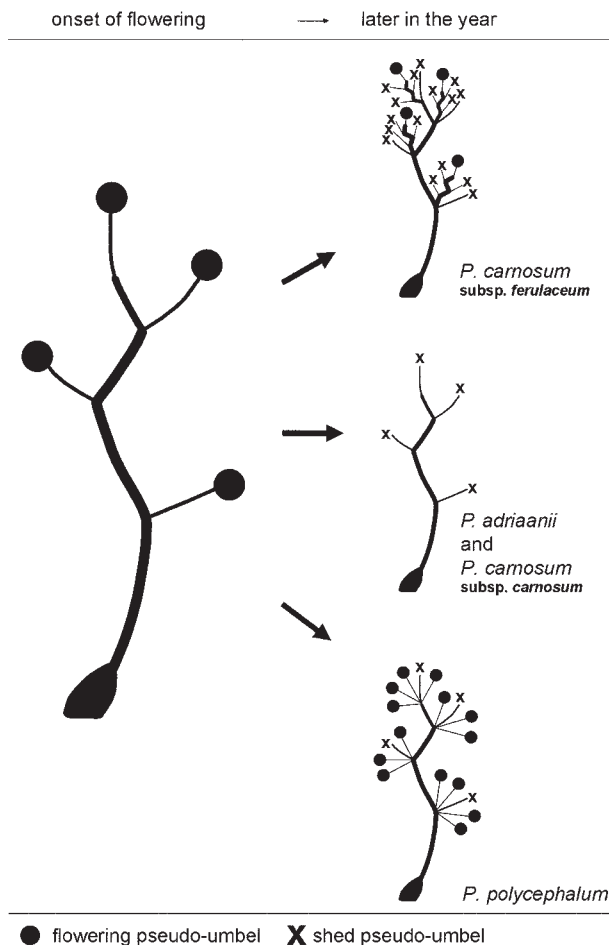


FIGURE 3.—Inflorescence branching patterns in *P. carnosum* complex. The inflorescence depicted to the left is the basal condition from which all taxa start at different times of the year. The drawings to the right (which are drawn to a smaller scale than the drawing to the left) represent three distinct inflorescence types at different times later in the year.

flowers each. The inflorescence of *P. carnosum* subsp. *ferulaceum* fits the overall pattern, but continues to produce further pseudo-umbels after the older flowers have already faded. The youngest pseudo-umbels are formed successively a few mm higher and higher; this leads to a delicately branched structure that resembles a panicle of grasses when not in flower. Individual inflorescences may last several months in *P. carnosum* subsp. *ferulaceum*. Due to its great vitality it may even produce vegetative shoots from the lower half of its inflorescence after flowering has ceased (not represented).

Pelargonium polycephalum likewise differs from *P. carnosum* subsp. *carnosum* and *P. adriaanii* by a larger number of pseudo-umbels. However, in contrast to *P. carnosum* subsp. *ferulaceum*, these do not emerge successively at the tip of the continuously growing peduncle, but develop in large numbers from already visible buds. Each of the 4 or 5 nodes of the principal axis may produce 10–15 pseudo-umbels with about 10 flowers each, which may add up to some 500 flowers per inflorescence within a relatively short period of time. Compared to *P. carnosum* subsp. *ferulaceum*, the life span of an inflorescence is short in *P. polycephalum*: the period between full flowering and fruiting and immediate with-

ering of the inflorescence will last a few weeks only. Hence, fully developed inflorescences are easily assigned to the respective taxa, but not young inflorescences, as these all represent variations of the same basic structural type.

Distribution and habitat

The four taxa in the *Pelargonium carnosum* complex occur within clearly circumscribed distribution areas which do not overlap much (Figure 4). *P. adriaanii* from the Northern Cape is geographically well isolated: there is no record of any other member of section *Otidia* within a radius of 50 km. Only a single plant resembling *P. parviflorum* is known from Kleinsee south of Port Nolloth (Drijfhout 2842 sub STEU2979). With the exception of a single disputed specimen, *P. adriaanii* has always been collected near the coast at altitudes of up to 50 m (Becker & Albers 2005a). *P. adriaanii* lodges at the fringes of the Gariiep Centre, which is a major centre of endemism (Van Wyk & Smith 2001) bordering on the southern Namib where the species receives less than 100 mm annual rainfall (Figure 4).

Pelargonium carnosum subsp. *carnosum* is exclusively found in the Western Cape within an area that stretches from the Atlantic coast to the chain of the Cedarberg–Swartruggens–Hexrivier Mountains at altitudes of up to 200 m. Receiving an annual rainfall of more than 300 mm, this region exhibits transitions to fynbos vegetation. The most typical specimens of *P. carnosum* subsp. *carnosum* are restricted to the Sandveld right at the coast. The two remainders in the *P. carnosum* complex occur further inland, receiving 150–250 mm of annual precipitation. The area of *P. carnosum* subsp. *ferulaceum* is largely situated in the Western Cape and stretches into the Northern Cape. The range of subsp. *ferulaceum* borders on the area of *Pelargonium carnosum* subsp. *carnosum*, but instead of proceeding to the Atlantic coast, stretches in the opposite direction towards the shrubland of the Great and Little Karoo. The subspecies occurs mostly at altitudes of 600–1 000 and in the vicinity of Vanrhynsdorp, merely at 100 m. *P. polycephalum* is largely restricted to the Namaqualand Hills in the Northern Cape Province at altitudes of up to 1 200 m.

Flowering phenology

As to the onset of flowering, there is a general cline in section *Otidia* running from north to south: taxa from the north (Namibia) exhibit an earlier blooming than their relatives from the south (Western Cape). This is particularly true for *Pelargonium ceratophyllum* L'Hér., *P. klinghardtense* R.Knuth and *P. paniculatum* Jacq. which already flower in early August. Although flowering starts at the same time in *P. laxum* (Sweet) G.Don from the Eastern Cape (receiving rainfall during summer), this species is subject to different environmental and climatic conditions. In most members of the *P. carnosum* complex, flowering starts not earlier than mid-September (*P. adriaanii*, *P. carnosum* subsp. *ferulaceum*) or early October (*P. carnosum* subsp. *carnosum*). The same is true for the taxa of the closely related *P. parviflorum* complex. With the exception of subsp. *karasbergense* (Becker & Albers in press a) which, similar to *P. laxum* occurs in

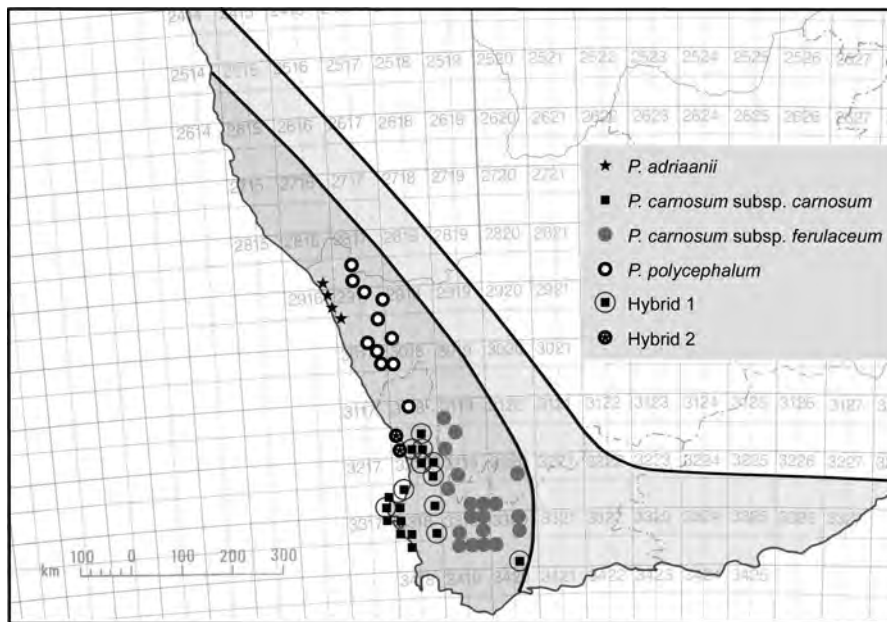


FIGURE 4.—Distribution of taxa in *P. carnosum* complex according to records from herbarium and living specimens. Dark grey shading = winter rainfall area; light grey shading = annual rainfall area.

the transitional zone between the winter and summer rainfall areas, flowering commences only from mid-September onwards in all subgroups of the latter complex—even including the taxa from Namibia. As was deduced from the collecting dates of dried specimens bearing flowers, *P. polycephalum* from the Namaqualand Rocky Hills is the only taxon in both complexes exhibiting a relatively early blooming. This species flowers from August to September. Hence, there is little overlap in the timing of the reproductive seasons of *P. polycephalum* and the remaining species in the *P. carnosum* complex and in the *P. parviflorum* complex. Onset and end of the flowering period may vary according to rainfall patterns; nevertheless, the sequence of ‘early’ and ‘late’ blooming taxa is maintained.

Morphological evidence of hybridization

Although the four taxa in the *Pelargonium carnosum* complex are clearly distinguished, the existence of intermediates is unmistakable. Interbreeding has repeatedly been recorded from areas where different taxa in the *P. carnosum* complex occur in close proximity.

Hybrids within the complex

The region west of the Cederberg (Vredendal–Clanwilliam) harbours hybrids between the two subspecies of *Pelargonium carnosum* which exhibit leaf features of both parental taxa (A&B4373). Plants from this area show the same type of indumentum as found in typical *P. carnosum* and pinnae as stalked and narrow as found in *P. carnosum* subsp. *ferulaceum*.

Plants from the coastal region near Papendorp and Doringbaai mostly exhibit pink petals (A&B4389, A&B4397). In this region, not less than three genotypes appear to intergrade, as the specific characters of all three taxa were found to combine in plants growing next to each other. These plants develop leaves as observed in *P. carnosum* subsp. *carnosum*, the distinct inflorescence of *P. polycephalum* and the long pedicels of *P. adriaanii*.

Hybridization involving taxa outside this complex

The closest relatives of the *Pelargonium carnosum* complex are found in the *P. parviflorum* complex. Structural intermediates occur in several regions which point to large-scale interbreeding between both complexes. The resulting cluster of hybrids are discussed elsewhere in more detail (Becker & Albers in press a) and are only briefly characterized in the present account. In this cluster of hybrids, floral structure is conspicuously varied exhibiting a range of petal colours and shapes.

The closest relatives of both complexes combined are *Pelargonium laxum* (Sweet) G.Don and *P. dasyphyllum* R.Knuth (Becker *et al.* 2008). Both species are clearly distinguished on account of a set of structural characteristics. *P. laxum* possesses posterior petals which are sharply reflexed from bases at nearly 180° and unusually long stamens. *P. dasyphyllum* exhibits a cushion-shaped growth habit and relatively small leaves. In both species, plants recorded from the geographical fringes also exhibit characters of the *P. carnosum* complex.

One record pertains to a plant of remote resemblance to *Pelargonium dasyphyllum* (A&B4286) which we tracked down in the midst of a population of typical members of that species. In this plant, the stem is unusually thickened and leaves are exceedingly large. The wide range of different petal shapes of individual specimens of *P. dasyphyllum* even includes the petal structure found in typical *P. carnosum* flowers.

Molecular analysis (AFLP)

The phylogram (Figure 5) results from a *neighbour joining* (NJ) analysis using 416 AFLP markers. Non-parametric bootstrap values (BVs) are indicated. A *maximum parsimony* analysis was also undertaken (not shown) employing 193 informative characters. The major groupings of taxa were congruent between both analyses.

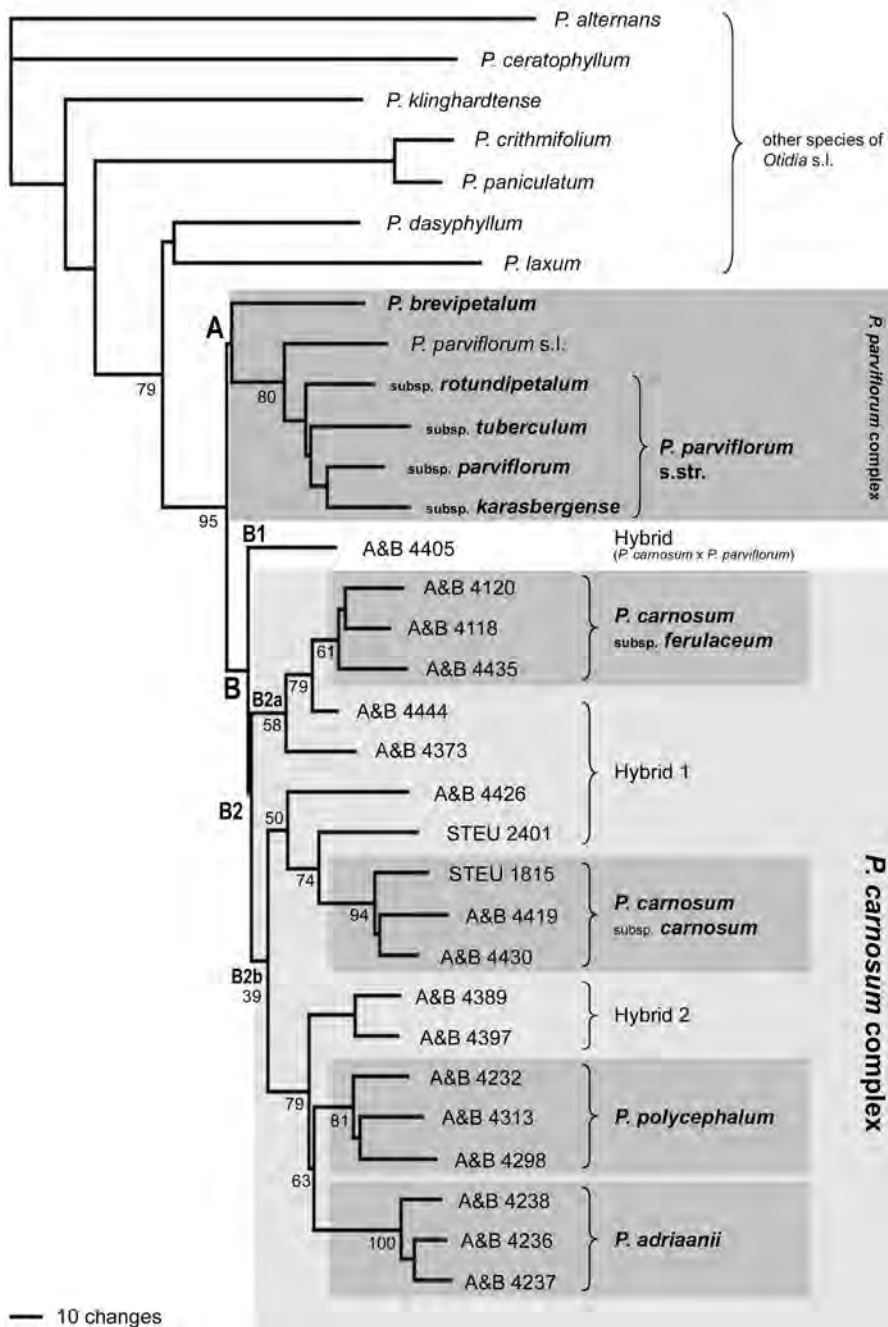


FIGURE 5.—Cladistic analysis of taxa in *P. carnosum* complex based on AFLP patterns; phylogenetic tree reconstructed by neighbour joining analysis using 416 AFLP markers. Bootstrap values derived from a maximum parsimony analysis employing 193 informative characters are indicated for clades that are congruent to the strict consensus tree. Collections that were unequivocally grouped under defined phenotypes of the complex are highlighted with dark grey shading.

There are three questions with regard to the *Pelargonium carnosum* complex: 1, is this complex a monophyletic group?; 2, are the distinct phenotypes reflected in distinct genotypes?; and 3, can the presumed existence of structural intermediates be verified?

Comparison with other members of section *Otidia* s.l. (*P. alternans*, *P. ceratophyllum*, *P. crithmifolium* Sm., *P. dasyphyllum*, *P. klinghardtense*, *P. laxum* and *P. paniculatum*) yields indications as to the monophyly of the complex. The study also involved the subspecies of the closely related *P. parviflorum* complex (Becker & Albers 2005b, in press a).

In the cladogram (Figure 5) the four taxa of the *Pelargonium carnosum* complex emerge as a single monophyletic group (clade B) with the *P. parviflorum* complex (clade A) as sister group. The clade that comprises

clade A and clade B is well supported by a BV of 95. With less good support (BV 79), *P. dasyphyllum* and *P. laxum* share a clade with the group that comprises clades A and B. Despite the many morphological signs of interbreeding between the two complexes, the typical phenotypes of *P. adriaanii*, *P. polycephalum* and subspecies of *P. carnosum* emerge as monophyletic groups (highlighted in dark grey in Figure 5). After excluding the samples of the supposed hybrids from the analysis, BVs rise to 95–100 in support of these groups (not represented in Figure 5). The cladogram seems to corroborate the presumed interbreeding processes among several taxa in the *P. carnosum* complex.

AFLP data are also consistent with the notion of phenotypic intergrades among the two subspecies of *Pelargonium carnosum* (Hybrid 1: A&B4444, A&B4373, A&B4426, STEU2401) and among *P. carnosum* subsp. *car-*

nosum/*P. polycephalum*/*P. adriaanii* (Hybrid 2: A&B4389, A&B4397). However, possible interbreeding processes also involve taxa in the *P. parviflorum* complex.

In terms of the grouping of taxa, one would expect both subspecies of *Pelargonium carnosum* to share one clade. However, subsp. *ferulaceum* appears in the cladogram as a sister group to clade B2b, which contains not only subsp. *carnosum* but also *P. polycephalum* and *P. adriaanii*. This may be seen as a conflict of molecular data and proposed taxonomy, which is based on morphology. On the other hand, this sister group relationship to the remaining taxa of the *P. carnosum* complex might reflect the ongoing gene flow between *P. carnosum* subsp. *ferulaceum* and the *P. parviflorum* complex, which has been predicted after evaluation of morphological traits.

Hybrid 1 comprises four plants in the cladogram that are supposed to result from gene flow between both subspecies of *Pelargonium carnosum*. As subsp. *ferulaceum* and subsp. *carnosum* do not share a clade, it is no surprise that the same is true for their hybrids.

The distribution areas of several taxa of the two complexes meet in the southern part of the Knersvlakte. In this area particularly, the two subspecies of *P. carnosum* and *P. parviflorum* s.l. appear to interbreed. Collection A&B4405 from Clanwilliam shows a phenotype similar to the intermediates of the two subspecies of *P. carnosum* (A&B4373, Vredendal population), but it is only one selected from an array of plants that intergrades to the *P. parviflorum* complex (Becker & Albers in press a).

DISCUSSION

Original descriptions

The distribution area of *Pelargonium carnosum* was assumed to be fairly large (Van der Walt 1977; Vorster 1990), since the delineation of *P. carnosum* subsp. *carnosum* was blurred, due to the occurrence of numerous intermediates. Furthermore, even taxa foreign to this complex were uncritically grouped under *P. carnosum* as well. However, when taxonomically treated in a stricter sense, *P. carnosum* is actually restricted to a comparatively small geographical area (Figure 4). This taxonomical concept is in line with Dillenius's original description of 1732 and the available herbarium records dating back to the first half of the 18th century both with respect to the morphological characteristics as well as to their geographical distribution.

With regard to the circumscription of *Pelargonium carnosum* subsp. *ferulaceum*, contradictions in the earlier descriptions (Burman f. 1759; Cavanilles 1787; Linnaeus 1826) led to a similar state of taxonomic limbo. This becomes obvious when comparing leaf characters given for '*P. ferulaceum*' and '*P. carnosum*', respectively (degree of division or separation of the leaf blade, degree of hairiness and succulence). Burman's iconotype of *P. ferulaceum* contains two variants of the same taxon which differ in leaf shape and (according to the diagnosis) in petal colour. The significance and reliability of this information can be questioned in view of Burman's

erroneous representation of the number of petals: the author believed both of his specimens to carry a single posterior petal and three or four anterior petals, which is not found in the genus *Pelargonium*.

So it happens that the view adhered to in the present account of '*Pelargonium ferulaceum*' not being synonymous to '*P. carnosum*' is based to a lesser degree on the original description (with the exception of leaf morphology) than on the extensive study of herbarium specimens, observations in the field and a molecular analysis of populations sampled from their natural habitats.

While the precise identity of the specimens on which '*Pelargonium ferulaceum*' were based remains obscure, the diagnosis of *P. polycephalum* is fairly straightforward. Although we could not examine the holotype itself (Drège 3244), we were able to study a comparable specimen (Drège 1033) which clearly showed the diagnostic features given in the original description for *P. polycephalum*: capitate pseudo-umbels and a panicle-like inflorescence. The notion of a conspicuous indumentum shown on the leaves remains incomprehensible. All dried and live specimens seen by us showed almost glabrous leaves.

Morphology and ecological function in a geographical context

Many structural differences between the taxa in the complex can be explained as adaptations to prevailing environmental conditions. With regard to leaf shape, two basic traits can be distinguished which correlate to the geographical distance from the coast. Plants occurring close to the sea exhibit virtually non-succulent and densely hairy leaves, whereas taxa from further inland are characterized by succulent and (to the naked eye) glabrous leaves. Another character shaped by habitat factors is the underground organs of the plants. *Pelargonium adriaanii* and *P. carnosum* subsp. *carnosum* occurring in Sandveld habitats near the Atlantic coast possess lateral roots with thickened sections, whereas the two taxa occurring further inland, *P. carnosum* subsp. *ferulaceum* and *P. polycephalum*, mostly on rugged soil, exhibit fibrous root systems lacking tubers.

Since the taxa in the *Pelargonium carnosum* complex are adapted to different climatic, edaphic and topographical factors and are associated with certain habitats, one could view them as mere ecotypes of a single taxon. However, this view is contradicted by the observation that *P. adriaanii* and *P. polycephalum* maintain their typical growth habit even under cultivation, and do not seem to hybridize on a large scale, which speaks in favour of treating them as separate species. While intermediates between *P. adriaanii*, *P. polycephalum* and *P. carnosum* were rarely recorded, the situation is different in '*P. carnosum*' and '*P. ferulaceum*'. In view of their extremely different habitats (Sandveld and Little Karoo) on the one hand and their relatively subtle structural differences on the other hand, it seems appropriate to treat them as subspecies. This view is supported by the occurrence of a range of phenotypic intermediates which is correlated to the distance from the sea and the immediate degree of aridity, respectively.

Molecular analysis and its taxonomic application

The results of the molecular analyses (AFLP) are mostly consistent with the hypotheses based on morphological observations. The four taxa in the *Pelargonium carnosum* complex emerge as a monophyletic group within section *Otidia* (Figure 5). *P. carnosum* subsp. *carnosum* and *P. carnosum* subsp. *ferulaceum* were treated as a single taxon by many authors (Van der Walt 1977; Vorster 1990), since neither their geographical range nor their morphological features were sufficiently known. Our molecular study confirms their close relationship but also provides evidence in favour of the existence of two distinct genotypes.

The close relationship of *Pelargonium adriaanii* and *P. polycephalum* as revealed by the AFLP analysis is surprising as there are profound differences in floral structure between *P. adriaanii* and *P. polycephalum*. Preceding the description of *P. adriaanii*, a short pedicel was among the diagnostic features given for the circumscription of the complex. The constricted pseudo-umbels of *P. polycephalum* versus the loose pseudo-umbels of *P. adriaanii* represent the extremes in this feature.

If the analysis is exclusively restricted to typical samples in the various taxa, high values are yielded in the *maximum parsimony* analysis and increased lengths of branches in the phylogenetic tree (not represented in Figure 5). The inclusion of all morphological intermediates demonstrates that interbreeding is the rule within the *Pelargonium carnosum* complex on the one hand (Figure 5) and among the *P. carnosum* complex and the closely related *P. parviflorum* complex on the other hand (Becker & Albers in press a).

Finally, the question arises: which taxonomic rank is appropriate in the *Pelargonium carnosum* complex? Following the biological species concept (Dobzhansky 1937), a species is a reproductive group; interbreeding among species is prevented by various isolation mechanisms. These include, in simple terms, mechanical, temporal, habitat-related and genetic barriers to interbreeding (Avice 2004). Mechanical isolating mechanisms, as brought about in the flower of different subgroups of *Pelargonium alternans* (Becker & Albers in press b), are absent in the *P. carnosum* complex. Despite differences in petal size and in lengths of pedicels, the taxa show basically the same floral structure.

In contrast, a seasonal isolation resulting from the development of different flowering periods is found in *Pelargonium polycephalum*. Nevertheless, a slight overlap of this species' reproductive season with that of *P. carnosum* subsp. *carnosum* results in the occurrence of hybrids in the region of Papendorp–Doringbaai (3118 CA and CC). Interbreeding between *P. polycephalum* and the cluster of hybrids in the *P. parviflorum* complex could also be expected due to their generally sympatric distribution and insufficiently separated flowering seasons. However, the occurrence of rudimentary and, consequently, sterile anthers in many '*P. polycephalum*' plants speak against consecutive interbreeding among *P. polycephalum* and *P. parviflorum* beyond the F1 generation (Becker & Albers in press a).

A habitat-related or geographical isolation is particularly found in *Pelargonium adriaanii*. While the distribution areas of the remainders in the complex border on each other, the range of *P. adriaanii* is situated fairly isolated in the region around Port Nolloth—as far as this can be assessed in view of the fact that we were unable to enter the local diamond mining area. From rare occurrences of *P. adriaanii*-like features near Papendorp, the existence of a gene substitution along the stretch of the Sandveld is presumed.

Intermediates between *Pelargonium carnosum* and *P. polycephalum* or *P. adriaanii* are on record, but such intermediates occur markedly less often than intermediates among the subspecies of *P. carnosum*. Since numerous morphological characteristics support the distinctness of their gene pools and as there are no indications of interbreeding processes going beyond the F1 generation, *P. polycephalum* and *P. adriaanii* continue to qualify as separate species. The position is completely different in the subspecies of '*P. carnosum*' and '*P. ferulaceum*'. Large-scale hybridization as in the region of Vredendal/Clanwilliam demonstrate the absence of effective reproductive isolation mechanisms; *P. ferulaceum* is therefore reduced to the rank of subspecies. There is evidence that *P. carnosum* subsp. *ferulaceum* is connected to *P. parviflorum* subsp. *parviflorum* via a full range of intergrading forms in the area of geographical overlap. In Becker & Albers (in press a) we will provide material that nonetheless supports the treatment of *P. parviflorum* and near related taxa as a distinct complex.

A recent breakdown of reproductive barriers resulting from human action as has been presumed by Vorster (1990) cannot be excluded, but such an assumption is not needed to explain the large number of interbreeding taxa. A shift in species distribution ranges due to recent climatic changes may have played a role.

As long as there is no artificial transport of propagules, the spread of settlements, agriculture, overgrazing and diamond mining could also isolate small populations from each other, as this would render large intermittent areas unsuitable to support the natural plant life. Nevertheless, man will hardly contribute to increase biotic diversity but rather destroy genetic diversity of the local flora as well as its natural habitats. *Pelargonium adriaanii* is currently threatened with extinction unless the diamond companies denounce their rights to fully exploit the diamond fields within the species' range.

The massive impact of human activities on the vegetation within the Cape floristic region is uncontested. Today the species-rich flora and fauna is protected within an increasing number of national parks and nature reserves. However, the Cape floristic region stands out in its wealth of endemics which often show a very localized distribution outside of protective areas. In order to protect even this species from extinction, centres of diversity have to be identified and plant diversity has to be put on record through taxonomic contributions. A further article on *Pelargonium* sect. *Otidia* will elucidate the unexpected radiation within the *P. parviflorum* complex, which hitherto has been treated as a single taxon.

SPECIMENS EXAMINED

Acocks 14847 (2b) K, PRE. Albers 2262, 2492 (2a) MSUN; 4174, 4175, 4176 (2b) MSUN. Albers & Becker 4235, 4236 (1) MSUN; 4184, 4185, 4186, 4382, 4383, 4384, 4385, 4410, 4411, 4412, 4413, 4414 (hybr. 1) MSUN; 4388, 4390, 4392, 4393, 4395, 4416, 4420, 4421, 4422, 4423, 4427, 4428, 4430, 4431, 4432 (2a) MSUN; 4461 (2b) MSUN; 4232, 4301, 4302, 4318, 4319, 4396, 4398 (3) MSUN. Albers, Becker & Strauch 4083, 4091, 4095, 4112, 4116, 4117, 4118, 4119, 4120, 4121, 4122, 4123 (2b) MSUN; 4081, 4084 (3) MSUN.

Bark s.n. (2a) K 74365. Bayer 1651 (3) NBG. Bolus 6531 (1) K, PRE; s.n. (2a) BOL107101, K74361; 13047 (2b) PRE; 446 = Herb. Bolus 6531 (3) BM, BOL, K. Boucher 2972 (2a) NBG; 2871 (2b) NBG, PRE. Bremer 363 (2a) PRE. Bultro 123 (hybr. 1) K. Chelsea Phys. Gdns s.n. (2a) BM649367, 649368.

Compton 8515 (2b) NBG; 6838, 17303 (3) NBG.

Dobay 59/75, 70/75, 79/75 (2b) NBG. Drake s.n. (2a) PRE 56350. Drège 7481 (2a) PRE; 01033 (3) PRE. Dreyer 39 (1) PRE. Drijfhout 1301 (2b) NBG, 2702 (2b) PRE.

Esterhuysen 1806 (2b) BOL; 22851 (2b) BOL, NBG; s.n. (2b) BOL 107074; 23593 (3) BOL. Euthen 2550 (hybr. 1) NBG.

Fischer 30 (2b) PRE.

Germishuizen 4811, 5311 (1) PRE. Gibby & Crompton 19 (hybr. 1) BM. Goldblatt 2395 (3) M, NBG, PRE.

Haftröm & Acocks 1986 (hybr. 1) BOL. Hall s.n. sub NBG. 98/68 (2b) NBG; 3475 (hybr. 2) NBG, PRE; 5260 (hybr. 2) NBG, PRE. Hardy 241 (2b) PRE. Hattingh 572/68 (hybr. 1) NBG. Herb. Regium Monacense s.n. (2a) M 36641, 36642, M 36643, 36644, 36645, 36646, 36647. Herre 2892, 7503 (2b) BOL; 2988 (3) BOL, K. Hugo s.n. (1) NBG 177505, PRE 650792.

Leighton 1243 (3) BOL. Leopoldt s.n. sub N.B.G. 1419/25 (2a) BOL; 19396 (2b) BOL; 3795 (3) BOL. Leistner 707 (2b) PRE; 2553 (3) K. Liede & Meve 619 (2b) MSUN.

Maguire 986 (3) NBG. Marloth 4026 (2a) PRE; s.n. (2a) PRE 56347; 8213 (2b) PRE; 12261 (3) BOL, NBG, PRE. Morris 5598 (3) K.

O'Call. & Steensma 1689 (2a) NBG. O'Callaghan 650 (hybr. 2) NBG. Odensen 1480 (hybr. 1) BOL.

Pearson 5301 (2b) K; 6487 (3) BM, K. Pienaar 1156 (1) PRE. Pillans 5626 (1) BOL, K; 6631, 6981 (2a) BOL.

Rechinger A3231 (hybr. 2) M.

Salter 1718 (2a) BM; 6465 (2a) BOL. Schlechter s.n. (1) NBG 177507; 1007 (3) PRE; 8199 (3) BM, K; s.coll. s.n. (2a) BM649375, 649379. Scully 196 (3) BOL. Stell. Univ. Gdns 2996 (2b) BOL. Stokoe 9541 (2a) PRE.

Taylor 12359 (hybr. 1) NBG; 7542 (2b) NBG.

Van der Walt 763 (hybr. 1) MSUN, PRE; 918 (2a) MSUN; 532 (2b) PRE; 1201 (2b) MSUN; s.n. (2b) PRE572097. Van der Walt & Vorster 1034 (hybr. 1) PRE. Van Jaarsveld s.n. (2b) NBG114903; 5704 (hybr. 2) NBG. Van Niekerk s.n. (2b) BOL107029. Vorster 2399, 2404 (2b) PRE.

Wagener 30 (2b) NBG. Ward 32, s.n. sub STEU3853 (2a) MSUN. Wilman 2316 (1) BOL. Wisura 584 (1) NBG; 268 (hybr. 1) NBG; 374, 1708 (2a) NBG; 2105 (2b) NBG.

ACKNOWLEDGEMENTS

We are indebted to the Department of Agriculture, Land Reform, Environment and Conservation of the Northern Cape and the Department of Fauna, Flora, CITES & Hunting of the Western Cape for granting collecting permits. The curators of the herbaria BM, BOL, K, NBG, and PRE are thanked for loans of numerous specimens.

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A review of the genus *Curtisia* (Curtisiaceae)

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Keywords: anatomy, Cornaceae, Curtisiaceae, *Curtisia dentata* (Burm.f.) C.A.Sm., revision, southern Africa

ABSTRACT

A review of the monotypic southern African endemic genus *Curtisia* Aiton is presented. Detailed studies of the fruit and seed structure provided new evidence in support of a close relationship between the family Curtisiaceae and Cornaceae. Comparisons with several other members of the Cornales revealed carpological similarities to certain species of *Cornus* s.l., sometimes treated as segregate genera *Dendrobenthamia* Hutch. and *Benthamidia* Spach. We also provide information on the history of the assegai tree, *Curtisia dentata* (Burm.f.) C.A.Sm. and its uses, as well as a formal taxonomic revision, including nomenclature, typification, detailed description and geographical distribution.

INTRODUCTION

Curtisia Aiton is a monotypic genus traditionally placed in the family Cornaceae. It is of considerable interest because of the many uses of its timber and bark—but no recent reviews of the morphology, taxonomy or anatomy are available. Recent cladistic and molecular systematic studies have revealed new evidence of relationships at family level (Murrell 1993; Xiang *et al.* 1993; Noshiro & Baas 1998; Xiang & Soltis 1998; Xiang 1999), including support for a separate family, Curtisiaceae, or a close relationship with the family Grubbiaceae, even resulting in a proposal for extending it to also include *Grubbia* P.J.Bergius (Xiang *et al.* 2002). As no taxonomic revision of *Curtisia* has ever been published since its original description in 1789, we present here a formal taxonomic treatment of this interesting southern African endemic genus. A further aim was to investigate the structure of the fruit and seeds to allow comparisons with putative relatives.

MATERIALS AND METHODS

Young branches with leaves and fruits at different stages of maturation were fixed in FAA (for a minimum of 24 hrs). The voucher specimen is *Van Wyk & Yembaturova 4218* (JRAU), collected at Diepwalle Forest (3323CC), Knysna District, Western Cape, South Africa. Some *Curtisia* fruits and seeds were also obtained from the carpological collections of LE and STU (collection of Felix Hohmann). Suitable portions were treated according to the method of Feder & O'Brien (1968) for embedding in glycol methacrylate (GMA). Specimens from the following herbaria were examined: JRAU, NBG, PRE and STU. Herbarium acronyms are given after Holmgren *et al.* (1990).

A Porter-Blüm ultramicrotome was used to cut transverse sections of the fruits from 3 to 5 µm thick, and the periodic acid-Schiff/toluidine blue staining method

(Feder & O'Brien 1968) was applied. Suitable sections were photographed. Fruits obtained from carpological collections were rehydrated and then softened by means of prolonged heating in Strassburger mixture (water, glycerol and 96 % ethyl alcohol in equal proportions), in accordance with traditional anatomical procedures (Prozina 1960) and then sectioned either by hand or sledge microtome. Test-reactions to identify lignification (phloroglucine and concentrated HCl), cutin and fatty substances (Sudan III, IV), starch (I-KI) and protein (biuret test with 5 % copper sulphate and 50 % KOH) were applied to the sections. The terminology used is illustrated in the figures.

RESULTS AND DISCUSSION

Vegetative morphology

The plants are tall shrubs or medium-sized trees 8 to 13 m high (Figure 1A) although specimens of up to 20 m are not uncommon (Coates Palgrave 2002). Young twigs are densely tomentose; the hairs are rusty brown to dark brown but become sparser and greyish with age. The bark is initially brownish and smooth; in older trees it becomes darker, tinted with grey and rough with square fissures (Figure 1D, E). The leaves are opposite, simple, petiolate and lack stipules. They are elliptic to ovate-lanceolate, 130–150 × 50–70 mm, leathery, bright to dark green and glossy above (but sometimes sparsely pubescent, mostly along the midrib, with simple, straight, thin hairs) and markedly reddish tomentose below (tending to become somewhat glabrescent with age). The lamina is entire, dorsiventral, with its apex broadly tapering to rounded and abruptly pointed; the base is mostly broadly tapering, less often cuneate; the margins are usually slightly revolute and are markedly dentate to serrate or almost sinuate. The venation is pinnate and markedly raised on the abaxial surface (Figure 1C). Stomata are anomocytic. Petioles are up to 30 mm long and rusty tomentose when young but may become sparsely hairy with age. Bud scales are brown or rust-brown and very densely pubescent.

Reproductive morphology and anatomy

Floral morphology and vasculature was thoroughly investigated by Eyde (1967, 1988). The small flowers of *Curtisia* are arranged in terminal, rather large (up to 120

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MS. received: 2008-03-28.

mm long) panicles (Figure 1B). Sometimes second-order inflorescences are formed of flowers clustered together, giving a somewhat capitate appearance. The peduncles and pedicels are covered with dense yellowish hairs. The opposite primary branches of the panicles are subtended by pronounced, markedly pubescent bracts (Cannon 1978). As is common for Cornaceae, floral parts are in fours (visible in Figure 1B). The petals are twice as long as the calyx tube, oblong in shape; the stamens are equal to petals in length. A characteristic centrally located vascular bundle in the four-loculed inferior ovary was described by Eyde (1967) who suggested the removal of *Curtisia* from Cornaceae on the basis of this feature.

Curtisia fruits (Figure 1C) are usually referred to as drupes (or 'drupaceous') (e.g. Dyer 1975; Leistner 2000) but this term is imprecise. True drupes are found only in the subfamily Prunoideae of the family Rosaceae where the fruit develops from a monocarpous gynoecium (Shibakina 1984; Levina 1987). In members of Cornales, as well as many other taxa, the fruits are syncarpous (with two or more fused carpels) and often pseudomonomerous (with only one of two or more locules and seeds reaching full development). Therefore, the term 'pyrenarium', proposed by Z. Artyushenko (Artyushenko & Fyodorov 1986) for such fruits as those of *Curtisia*, will be used. The term 'pyrene' applies to fruits

such as those of *Ilex* L. and some Araliaceae, where each seed is surrounded by a lignified endocarp (each called a pyrene). However, when the endocarp is fused into a single bony structure around the seeds, the term 'fused pyrenes' or 'pyrenarium' is preferable. The pyrenaria of *Curtisia* are small (10–15 mm in diameter), globose, subglobose or rarely ovoid, snow-white and sometimes with $\pm$ persistent calyx teeth (Figure 1C). The outer pericarp tissues are fleshy (Figure 2A) and comprise both hypanthial exocarp and mesocarp, the latter developed from both hypanthial and carpellary tissues. The heavily lignified endocarp constitutes a four-loculed stone, usually with a fully developed seed in each. Only the very central area, where the vascular bundle is located, is not lignified (Figure 2F, arrow). The seeds are exotestal (see description of the seed coat later on), with copious endosperm and a well-developed, small, centrally located embryo.

The structure of the fruit wall and the seed was studied in detail. The exocarp is formed by a single layer of radially elongated cells with heavily thickened and cutinized walls (Figure 2B). The mesocarp is primarily parenchymatous. A hypoderm is clearly visible (Figure 2B, K) as the outermost zone of the mesocarp, with two to three layers of minute cells which are flattened in the tangential direction and sometimes have an almost

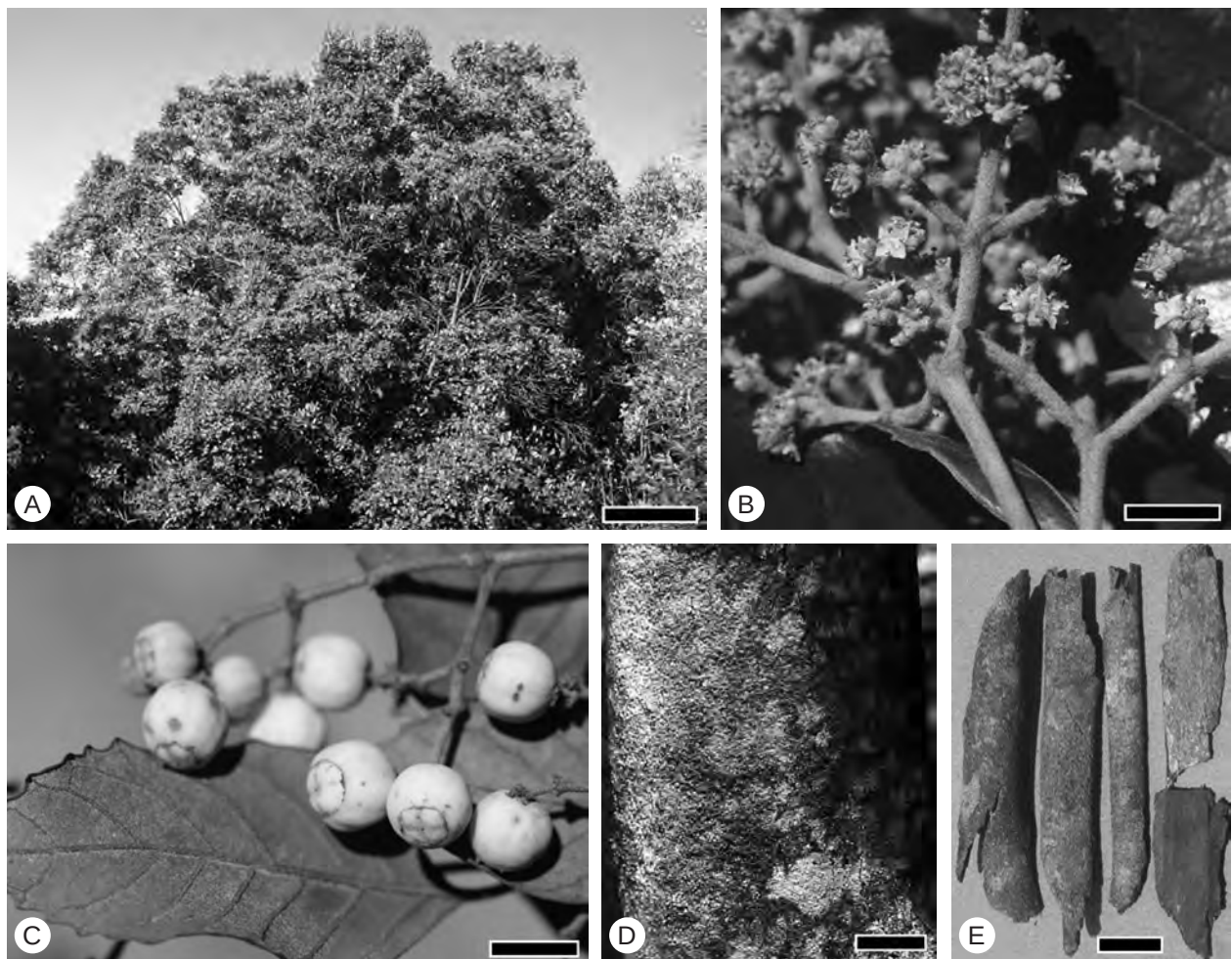


FIGURE 1.—Morphology of *Curtisia dentata*: A, growth form (cultivated tree at Kirstenbosch Botanical Garden); B, inflorescence with flowers (note densely tomentose vestiture); C, fruits (note white colour) and leaf surface; D, E, bark. Scale bars: A, 1 m; B, 6 mm; C, 10 mm; D, E, 40 mm. Photographs by B-E. van Wyk.

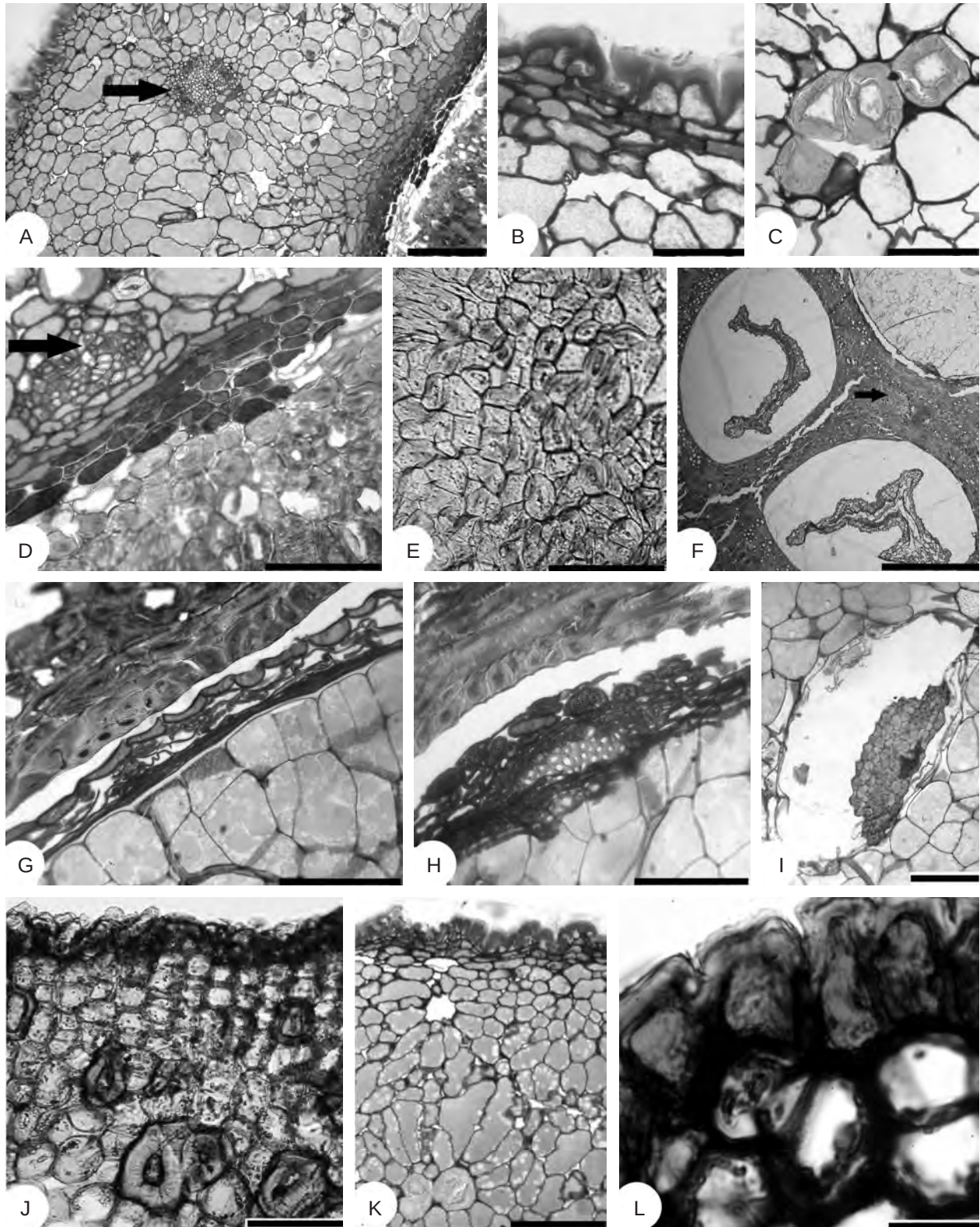


FIGURE 2.—Fruit and seed anatomy in c/s: A–I, K, *Curtisia dentata*; J, L, *Dendrobenthamia japonica* (Sieb. et Zucc.) Hutch. A, fleshy part of pericarp; B, exocarp (note cell wall cutinization) and hypoderm (outermost zone of mesocarp); C, mesocarp sclereids; D, derivatives of mesocarp vascular bundles and transitional zone between mesocarp and endocarp; E, endocarp sclereids; F, endocarp with seed-bearing locules and central vascular bundle (arrow); G, seed coat; H, seed coat vascular bundle; I, embryo and endosperm cells; J, K, exomesocarp with scattered sclereids (note similarity in structure); L, exocarp cells. Scale bars: A, J, K, 0.2 mm; B–E, G–I, L, 0.07 mm; F, 0.7 mm.

tabular arrangement. Most of the mesocarp consists of loosely arranged, large, thin-walled parenchymatous cells of varying shape. These cells form up to 16 layers. Small sclereids (Figure 2C) can be found scattered throughout the entire mesocarp (solitary or in clusters of two to

four). Also scattered in the mesocarp are the derivatives of vascular bundles (Figure 2A, D, arrow); they are fairly large but usually only slightly lignified. The inner zone of the mesocarp is composed of two or three layers of small, thin-walled cells which are elongated tangentially.

There is a very conspicuous intermediate zone between the mesocarp and endocarp, formed by five to seven (or up to nine) layers of small, tangentially elongated cells filled with brightly coloured tanniniferous substances (dark zone in Figure 2A, D). These cells possess slightly thickened walls that are somewhat lignified.

The typically woody endocarp comprises 17 to 20 layers of fairly small sclereids (Figure 2E), mostly orientated parallel to the longitudinal fruit axis, except for the innermost layer(s), which can be variously orientated to form a 'lining' layer for each locule. Some of the sclereids appear to contain tannins.

The seed coat of *Curtisia* was previously incompletely described as 'thin and filmy, made of compressed and partially obliterated cells' (Trifonova 2000). However, our study revealed several interesting structural details. Firstly, the exotesta is composed of fairly large, tangentially elongated cells, which appear oval or almost crescent-shaped in cross section (due to concave outer tangential walls) (Figure 2G). These cells are filled with tanniniferous substances and have walls consisting of cellulose. In certain parts of the seed coat, large sclerified vascular bundle derivatives are found (Figure 2H), surrounded by a few layers of very small, compressed parenchymatous cells. This type of seed coat can be classified as 'exotestal' because of the pronounced, thick-walled outer cells.

The meso- and endotestal components of the seed coat largely consist of compressed and deformed cells of irregular shape, sometimes only with their walls persisting. The part of the endotesta which lies against the endosperm is homogenous and the cell walls are indistinguishable and cutinized.

The seed has a massive copious endosperm, with protein as the main ergastic substance; the minute embryo is located centrally within the endosperm (Figure 2I).

Phylogenetic relationships

The relationships of *Curtisia* have not yet been clarified. Its position within the Cornaceae had been stable for a long time (Harms 1898; Wangerin 1910; Philipson 1967; Cronquist 1981; Thorne 1992) but its isolated position within the family was noted—hence the subfamily Curtisiaceae of Harms (1898). Evidence had gradually accumulated (Adams 1949; Eyde 1967; Yeramyan 1971) for separating it as a monotypic family Curtisiaceae Takht. (validated by Takhtajan 1987) but still within Cornales. This followed an earlier trend of splitting the broad family concept of Harms (1898) by elevating most of the 15 genera to family status, e.g. *Davidia* Baill. to Davidiaceae (Li 1954), *Mastixia* Blume to Mastixiaceae (Calestani 1905—cited by Takhtajan 1987) and *Toricellia* DC. to Toricelliaceae (Hu 1934—cited by Takhtajan 1987).

Detailed molecular systematic studies by Xiang and co-authors (Xiang *et al.* 1993, 1998, 2002; Xiang & Soltis 1998; Xiang 1999; Fan & Xiang 2003) showed that *Curtisia* is sister to another southern African endemic genus *Grubbia*, and that the combined clade is again sister to the rest of the Cornales. A suggestion by Xiang *et al.* (2002) to expand the Grubbiaceae to include

Curtisia (citing similarities such as the geographical distribution, woody habit, leathery simple leaves with revolute margins, opposite phyllotaxy, lack of stipules, hermaphroditic flowers, inferior ovary and copious endosperm) was not followed in later treatments (e.g. Angiosperm Phylogeny Group II 2003; Heywood *et al.* 2007) where the two monotypic families were retained. According to Xiang *et al.* (2002), 'no apparent morphological synapomorphies can be found for the two genera at present' and there are indeed important differences between them. The distribution of *Curtisia* extends along the southern and eastern coast of South Africa northwards as far as Mozambique (coastal zone—Da Silva *et al.* 2004) and eastern Zimbabwe (Baker 1911–1912; Eyles 1917), whereas *Grubbia* is restricted to fynbos. The large, leathery leaves of *Curtisia* are coarsely dentate or sometimes sinuate and only slightly revolute, whereas the small, almost ericoid leaves of *Grubbia* species have entire margins which are distinctly revolute. There are also important morphological differences in reproductive structures—inflorescences, flowers and especially the fruits. Xiang *et al.* (2002) ascribed these differences to ancient divergence. It is possible that a more detailed investigation of the anatomy of *Grubbia* fruits and seeds could shed some light on the *Curtisia*–*Grubbia* relationship, but hitherto this appears to be based only on molecular evidence.

Carpological research of Cornales and allies by Yembaturova (2001, 2002), the comparative results of which are summarized in Table 1, showed a number of basic structural traits that appeared to be of diagnostic value. *Curtisia* resembles *Cornus* L. s.l., *Nyssa* L., *Alangium* Lam. and *Corokia* A.Cunn. most closely, and *Davidia* and *Mastixia* to a lesser extent. All of these taxa have epigynous flowers (however, this is still questionable for *Davidia*), typical pyrenaria, thick, succulent exomesocarps and well-developed woody endocarps. *Curtisia*, however, differs from all other taxa in having stones with all four locules similar in size and shape, each containing a fully developed seed. The other taxa usually have only a single fully developed locule and seed. There are also differences in some finer structural details. *Alangium* and *Mastixia*, for example, have conspicuous secretory structures in their fleshy mesocarp tissues which are absent in *Curtisia*. Species of *Nyssa* have either no sclereids or far more mesocarp sclereids than *Curtisia*. Furthermore, *Curtisia* is the only genus with a centrally located vascular bundle in the ovary; other putative Cornaceae relatives are reported to have transseptal bundles (Eyde 1967).

As is well known, the Cornaceae have a rich fossil record which includes wood, leaves and especially fruits (Miki 1956; Eyde & Barghoorn 1963; Eyde *et al.* 1969; Mai & Walther 1978; Arbuzova 1988; Eyde 1988; Eyde & Xiang 1990). Most of the fossil structures have been identified as belonging to the genera *Davidia*, *Mastixia*, *Diplopanax* Hand.-Mazz., *Nyssa*, *Alangium* and *Cornus*. Recently, a fossil species of the Eocene London Clay flora, originally referred to as *Leucopogon quadrilocularis* Reid & Chandler or *Cornus quadrilocularis* (Reid & Chandler) Chandler was shown to belong to *Curtisia* (Manchester *et al.* 2007) on the basis of the endocarp structure. The fossil endocarps of *Cornus quadrilocula-*

ris are composed of slightly elongated sclereids and possess four seed-bearing locules and a vascular bundle in the centre, as in extant *Curtisia*.

The greatest degree of resemblance to *Curtisia* in pericarp structure (Figure 2J, L, with a portion of *Curtisia* pericarp given in Figure 2K for comparison) is shown by two representatives of the genus *Cornus* s.l., currently segregated into the genera *Dendrobenthamia* (Asian dogwoods with compound fruits) and *Benthamidia* (American dogwoods with fruits clustered together without fusing). These three taxa all have radially elongated exocarp cells with heavily cutinized walls, solitary or clustered sclereids scattered throughout the parenchymatous mesocarp and a homogeneous woody endocarp. It is noteworthy that scattered sclereids were previously treated as an adaptation to synzoochorous dispersal in the relatively large, compound fruits of *Dendrobenthamia*, believed to be dispersed by monkeys (Eyde 1985). *Curtisia* fruits, despite their bitter taste, are also dispersed by animals such as birds (loeries, rameron pigeons), wild pigs, monkeys and less often baboons (Watt & Breyer-Brandwijk 1962). It seems likely that *Curtisia* fruits may be oil-yielding, as many white-fruited dogwoods from *Cornus* s.l. [e.g. *Swida alba* (L.) Opiz, *S. sericea* (L.) Holub and other shrubby species] have fruits rich in oil (Sozonova 1992). These fruits look white because of the oil droplets that reflect light. Thus, fruit anatomy has hereby provided evidence of a possible *Curtisia*–*Cornus* affinity and therefore supports Takhtajan's (1987) treatment of *Curtisia* as a monotypic family Curtisiaceae within the order Cornales, close to the core family Cornaceae. The latter is currently treated as consisting only of *Cornus* s.l. but it has often been divided into several segregates (Takhtajan 1987, 1997).

TAXONOMY

***Curtisia* Aiton**, Hortus kewensis 1: 162 (Aug.–Oct. 1789) nom. cons.; Thunb.: 100 (1792); Thunb.: 28 (1794); Thunb.: 141 (1823); Willd.: 687 (1797); Roem. & Schult.: 294 (1818); Spreng.: 442 (1825); DC.: 12 (1825); Harv.: 143 (1838); Endl.: 799 (1839); Lindl.: 783 (1847); Harv.: 579 (1862); Hook.f.: 949 (1867); Baill.: 3: 334 (1863), 163 (1879a), 253 (1879b); Harms: 262 (1898); Wangerin: 29 (1910). Type: *C. faginea* Aiton [now *C. dentata* (Burm.f.) C.A.Sm.].

Note: the generic name *Curtisia* Aiton was conserved against the earlier homonym *Curtisia* Schreber, Apr. 1789 (family Rutaceae) and is listed in the International Code of Botanical Nomenclature (McNeill *et al.* 2006). Both these generic names were given in honour of William Curtis, the founder and for a long time the proprietor of the famous *Curtis's Botanical Magazine*, published since 1786 and known as *Botanical Magazine* (Burt Davy 1932; Marais 1985).

Trees, medium-sized to large, up to 20 m high, or tall shrubs. Bark brown and smooth when young, dark brown and square-fissured with age. Young branchlets with reddish or rust-brown hairs. Leaves simple, opposite; petiole up to 20(–30) mm long, pubescent; lamina oblong-elliptic to ovoid, 25–10 × 25–75 mm, penninerved, leathery, margins dentate, revolute to sinuate, glabrous on upper surface and rust-brown pubescent beneath. Inflorescences terminal, paniculate, loose or compact, inflorescence branches tomentose; bracts conspicuous, linear-lanceolate, rust-brown tomentose, subtending opposite primary inflorescence branches. Flowers minute, sessile or shortly pedicellate, scentless, hermaphrodite, epigynous, tomentose. Calyx tube 4-lobed, adnate to ovary. Petals 4, cream-coloured or white with a tint of purple, valvate. Androecium didymous; stamens 4, alternating with petals; filaments subulate; anthers short. Gynoecium syncarpous; ovary 4-locular (occasionally 3-locular); ovules pendulous, one per locule. Fruit globose, snow-white, drupaceous (pyrenarium), stone

TABLE 1.—Comparative carpological traits in genera of Cornaceae sensu Harms (1898) [From Yembaturova (2001), translated from Russian]

Taxa	Ovary	Mature pericarp consistency	No. well-developed seeds per fruit	Endocarp type and no. cell layers	No. locules or pyrenes	No. and type of sterile locules	No. mesocarp cell layers
1. <i>Cornus</i> L.	Inferior	Fleshy	1 or 2	Woody (> 20)	1 or 2 (3 or 4) locules	1(2), compressed	> 20
2. <i>Nyssa</i> L.	Inferior	Fleshy	1 or 2	Woody (> 20)	1 or 2 locules	1, compressed	> 20
3. <i>Alangium</i> Lam.	Inferior	Fleshy	1 or 2	Woody (> 20)	1 or 2 locules	1, compressed	> 20
4. <i>Mastixia</i> Blume	Inferior	Fleshy	1	Woody (16–20) (transition to cartilaginous)	1 (incomplete septa)	None	> 20
5. <i>Corokia</i> A.Cunn.	Inferior	Fleshy	1 or 2	Woody (> 20)	1 or 2 locules	None	> 20
6. <i>Davidia</i> Baill.	Inferior (?)	Fleshy	1	Very woody (> 20)	7–9 locules	6–8 compressed	> 20
7. <i>Curtisia</i> Ait.	Inferior	Fleshy	4	Woody (> 20)	4 locules	None	> 20
8. <i>Camptotheca</i> Decne	Inferior	Dry at maturity	1	Weakly lignified, reduced (7–8)	1	None	> 20
9. <i>Griselinia</i> Forst.f.	Inferior	Fleshy	1	Weakly lignified or non-lignified (3–7)	1	None	17–20
10. <i>Aucuba</i> Thunb.	Inferior	Fleshy	1	Non-lignified (3–5)	1	None	15–18
11. <i>Toricellia</i> DC.	Inferior	Fleshy	1	Cartilaginous (12–14)	3 or 4 locules	2 or 3, keep their shape and size	6–9
12. <i>Melanophylla</i> Baker	Inferior	Dry at maturity	1	Woody	3 locules	2, keep their shape and size	few
13. <i>Kaliphora</i> Hook.f.	Semi-inferior	Fleshy	2	Cartilaginous (7–8)	2 pyrenes	None	> 20
14. <i>Helwingia</i> Willd.	Inferior	Fleshy	2–4	Cartilaginous (6–10)	2–4 pyrenes	None (rarely 1)	20
15. <i>Garrya</i> Dougl. ex Lindl.	Superior	Dry at maturity	1 or 2	Non-lignified (2–7)	1	None	10–13

(3)4-locular, (3)4-seeded, with a central vascular bundle. *Seeds* exotestal. *Endosperm* copious. *Embryo* minute, centrally located. *Flowering time*: late October to March. *Fruiting time* May to October. *Chromosome number* $n = 13$ (Goldblatt 1978). *Conservation status*: Low Risk. Figure 1.

The species of Curtisia

There is only one extant species in the genus (see generic description given above).

***Curtisia dentata* (Burm.f.) C.A.Sm.**, in Journal of South African Forestry Association 20: 50, t. 170 (1951); Cannon: 635 (1978). Type: South Africa, *Sideroxylum dentatum* J.Burm., Rariorum Africanarum plantarum 235, t. 82 (1738), iconotype (Figure 3).

Sideroxylon dentatum Burm.f.: 6 (1768).

Curtisia faginea Aiton: 162 (1789); Willd.: 687 (1797); Roem. & Schult.: 294 (1818); Thunb.: 141 (1823); Spreng.: 442 (1825); DC.: 12 (1825); Pappe: 17 (1854); Harv.: 570 (1862); Wangerin: 30 (1910); Baker f.: 76 (1911–1912); Eyles: 435 (1917); Burt Davy: 512 (1932); Steedman: 60 (1933). Type: South Africa, introduced by Francis Masson in 1775 (Banks Herbarium, sheet BM000794113, BM!).

Illustrations: Burm.: t. 82 (1738); Lam.: t. 71 (1823); Sim: t. 77 (1907); Wangerin: 30 (1910); Burt Davy: 513 (1932); Cannon: t. 170 (1978). There is a beautiful unpublished painting of *Curtisia dentata* by Clemenz Heinrich Wehde mann (1762–1835) in the repository of Natural History Museum (BM). This original watercolour forms part of the Wehde mann collection entitled 'Sketches of plants growing about Plattenburg Bay on the coast of Africa'.

History and uses

The most well-known name for *Curtisia* is assegai, assegai-tree (Afrikaans: *assegaaiboom*) or assegai-wood (*assegaaihout*). The records for this name date back to the earliest colonial days, recorded, according to Smith (1966), by Hermann in 1672 and Burmann in 1692. These plant names apparently were the first cases of modern spelling of the name. Early writers used such versions as *hazegaiejn boomen hout*, *assgaaij*, *assegaie* and *hassagay-hout*. As far as the origin of the name *assegai/assagay* is concerned, several versions exist. One of them is that the name is derived through Portuguese from the Latin word *hasta*, meaning a spear (Palmer & Pitman 1972). Another idea is that it refers to the Arabic word *Azzaghayah*, adopted by the Portuguese with various spelling modifications and taken over by early Dutch writers (Smith 1966), evolving to its present-day form with time but always referring to weapons (spears and bows) used by the native African people. The ethnobotanical importance of the tree is reflected in the large number of vernacular names recorded in southern Africa. In Table 2, all these are listed exactly as they were published.

The wood of *Curtisia* is iron-hard but elastic, strong and very durable—traditional javelins and spears, with 1.8 m-long tapering shafts, were made from this timber. Thunberg, in his descriptions of his travels in the Cape of Good Hope between 1772 and 1775 (Forbes 1986), repeatedly mentioned *Curtisia* (as 'assagay wood') and its practical use for 'assagays' (javelins that Khoikhoi people carried with them on their journeys, with which they 'defended themselves against their enemies and wild beasts, and were able to kill them, buffaloes and other animals'). Later on, many other uses were found. The fact that assegai wood shrinks less than most

other woods, made it very useful for the early settlers. It was the preferred timber for the axles and poles for wagons as well as the spokes, naves and felloes of the wheels. The highly decorative qualities of *Curtisia* timber—resembling mahogany due to developing a reddish brown, cinnamon tint with age—were appreciated by craftsmen producing tool handles (hammer handles in particular), implements of husbandry, furniture and floor covering (Watt & Breyer-Brandwijk 1962; Smith 1966; Palmer & Pitman 1972; Van Wyk *et al.* 2000). The bark was used for tanning, yielding 2.98 to 14.05 % of tannin; up to 4 % of tannin was yielded by the leaves and twigs of the plant (Watt & Breyer-Brandwijk 1962; Van Wyk *et al.* 1997). *Curtisia* is also an attractive ornamental tree, especially for moist gardens.

Curtisia dentata is important in traditional medicine (Arnold *et al.* 2002). Zulu people use the bark to treat diarrhoea and stomach ailments. It serves as an aphrodisiac (a 'love charm' to make a man attractive) and as a 'blood purifier' or 'strengtheners' (Cunningham 1988; Hutchings *et al.* 1996; Van Wyk *et al.* 1997; Ngwenya *et al.* 2003). Since the tannin-rich bark is used for medicinal purposes, the debarking and ringbarking of trees caused significant damage in some localities. The bark (Figure 1E) used to be sold by traditional Zulu herb gatherers for R30 per 50 kg bag but after becoming scarce due to overexploitation, it is only included in special bark mixtures, such as 'Special Khubalo' (Cunningham 1988). Rapid coppicing and the apparent capability of the bark to regrow, played a very important role in the survival of this forest tree. Despite a broad phytochemical survey of the Cornaceae by Bate-Smith *et al.* (1975), the chemical rationale for the traditional uses is still poorly understood. It may be assumed, however, that the high tannin content contributes to the efficacy in treating diarrhoea and stomach ailments.

Geographic distribution

Curtisia dentata is restricted to southern Africa, primarily along the southern and the eastern coasts of South Africa and extends into Swaziland, Mozambique and eastern Zimbabwe (Figure 4). The genus is confined to montane forests (mainly found on southern and southwestern slopes), at altitudes from sea level to 2 300 m.

SPECIMENS EXAMINED

Anon. 9701 (PRE). A.M.W. 1005 (NBG). Acocks 8992 (PRE). Airy Shaw 3614, 3736 (PRE).

Bakker 281 (PRE). Balkwill 1474 (PRE). Balsinhas 02576 (PRE). Bayliss 127, 6169 (PRE, 2 sheets); 466, 1328, 1490 (PRE). Bazer 809 (PRE). Bird 1042, 1213, 1241, 1396, 1412 (PRE). Bos 965 (NBG, PRE); 1314 (NBG). Botha 0007 (PRE). Botha & Cilliers 3636 (PRE). Boucher G19, 322, 2078 (PRE). Bredenkamp 1511 (PRE). Britten 1333 (PRE). Burgers 1111 (PRE). Burgoyne 1726 (PRE); 6206 (NBG, PRE). Burt Davy 1262, 2439, 2442 (PRE).

Cheadle 737 (PRE). Codd 3050 (PRE). Codd & Dyer 9117 (PRE). Comins 933 (PRE). Compton 28675, 32241 (PRE); 29500 (NBG, PRE). Curson & Irvine 86 (PRE, 2 sheets).

Dahlstrand 2661 (PRE). Davis 56 (PRE). De Winter 8266A (PRE). Dlamini s.n. (PRE). Dohse 140 (PRE). Duthie 632 (NBG). Dyer 4850 (PRE).

Eastwood 2430 (PRE). Ecklon & Zeyher 558 (NBG, 2 sheets); 596 (NBG); s.n. (PRE). Edwards 1450, 3311 (PRE).



FIGURE 3.—Iconotype of *Curtisia dentata* [Burmamn: plate 82 (1738)].

Fisher 1105 (PRE). Flanagan 143 (PRE). Forest Dept. s.n. sub STEU18857 (PRE).

Galpin 4229, 11612, 13676 (PRE). Gertzner 4387, 4488, 4499 (PRE). Giffen G849 (PRE). Gillet 72, 1311 (NBG). Glen 2413 (PRE). Goodier & Phipps 157 (PRE). Grant 3263 (PRE). Guillarmod 9314 (PRE).

Hemm 40, 522 (PRE). Henkel 2545 (PRE). Herman & Prior 322 (PRE). Hoffmann 171 (PRE). Humbert 9675 (PRE).

Jacobsen 1812, 4679 (PRE). Jones & Leach 2531 (PRE).

Kemp 1200 (PRE). Kerfoot 6122 (PRE, 2 sheets; STU). Kerfoot, Forrester & Gooyer 131 (PRE). Killick 866, 1900 (PRE); s.n. (PRE, photo!). Kluge 1358 (PRE).

Legat 2442 (PRE). Liebenberg 7955A (PRE).

MacOwan 731 (PRE). Maguire 1438 (NBG). Marloth 524 (PRE); 5246 (NBG). Meyer 1927, 2610 (PRE). Miller S/26 (PRE). Muir 117 (PRE). Mogg 17209, 34609 (PRE). Mohle 416 (PRE). Moll 1789 (PRE). Morze 2010 (PRE). Mullin 16/52 (PRE). Mullins s.n. (PRE, 2 sheets). Müller 487 (PRE). Müller & Scheepers 118 (PRE).

Nicholson 658 (PRE). Nienaber EN162 (PRE).

Obermeyer 890, 1179 (PRE); 2008 (NBG, PRE). Osborne 30 (PRE).

Paterson 2109 (PRE). Pegler 1332, 4606 (PRE); s.n. (NBG). Phillips s.n. (PRE). Pillans 3664 (PRE). Plantk. Hons. 477 (JRAU). Pole Evans 3619, 15490, s.n. (PRE). Prosser s.n. (PRE).

Raal 226 (PRE). Ranger 290 (PRE). Reid 4063 (PRE). Reyneke 189 (PRE). Rodin 3147, 4104 (PRE). Rogers 23038 (PRE). Rudatis 1776 (PRE).

Scharf 1784 (PRE). Scheepers 832 (PRE). Schutte 29 (JRAU). Sebothoma 334, 346 (PRE). Sim 2020 (PRE). Smith 40 (PRE). Smuts 11, 98 (PRE); 1094 (PRE, 2 sheets); s.n. (NBG). Smuts & Gillet 2262 (NBG, PRE); 3600 (PRE). Stalmans 335, 1164 (PRE). Stokoe s.n. (NBG). Stork 61580 (PRE). Story 1665 (PRE). Strey 9424, 10738 (PRE). Symons 504, 15736 (PRE).

Thode A273 (PRE); A844 (NBG, PRE); A845 (PRE, 2 sheets). Thorncroft 1005 (PRE). Topper 97 (NBG). Torre & Pereira 12.738 (PRE).

Uys s.n. (PRE).

TABLE 2.—Vernacular names for *Curtisia dentata*. All names given in exactly same form as originally published

Vernacular name	Language group	Reference
Assegaaiboom; assegaaihout; (Assegaa wood)	Afrikaans	Hutchings <i>et al.</i> 1996; Smith 1966; Von Breitenbach <i>et al.</i> 2001
Assegaa-hout	Afrikaans	Burt Davy 1932
Assegaa	Afrikaans	Coates Palgrave 2002; Hutchings <i>et al.</i> 1996; Van Wyk <i>et al.</i> 1997, 2000; Von Breitenbach <i>et al.</i> 2001
Asgaa	Afrikaans	Von Breitenbach <i>et al.</i> 2001
Asgaa hout	Afrikaans	Burt Davy 1932; Watt & Breyer-Brandwijk 1962
Assegai	English	Coates Palgrave 2002; Van Wyk <i>et al.</i> 1997, 2000; Von Breitenbach <i>et al.</i> 2001
Assegai wood	English	Watt & Breyer-Brandwijk 1962
Assegai-tree	English	Coates Palgrave 2002
Cape assegai wood	English	Steedman 1933; Watt & Breyer-Brandwijk 1962
Lance wood	English	Steedman 1933; Watt & Breyer-Brandwijk 1962
muchekamani	Ndau	Watt & Breyer-Brandwijk 1962
Muchekamani	Ndau	Steedman 1933
umquixina	Nguni	Watt & Breyer-Brandwijk 1962
modula-tšhwene	Northern Sotho	Palmer & Pitman 1972
Modulatšhwene	Northern Sotho	Von Breitenbach <i>et al.</i> 2001
Molowla-tchayne	Ses.	Burt Davy 1932
Mubotjo; mupunguti	Shona	Watt & Breyer-Brandwijk 1962
iliNcayi; isiNwati	Swazi	Palmer & Pitman 1972
ili-ncayi; isi-nwati	Swati	Watt & Breyer-Brandwijk 1962
um-poyi	Swati	Watt & Breyer-Brandwijk 1962
musangwe; mufhefhera	Venda	Palmer & Pitman 1972
umGzina	Xhosa	Palmer & Pitman 1972
umgxina	Xhosa	Von Breitenbach <i>et al.</i> 2001
umhlebe	Xhosa	Von Breitenbach <i>et al.</i> 2001; Watt & Breyer-Brandwijk 1962
omhlebe	Xhosa	Watt & Breyer-Brandwijk 1962
isibande; usirayi	Xhosa	Von Breitenbach <i>et al.</i> 2001
umlahleni	Xhosa	Van Wyk <i>et al.</i> 1997
umhlibe	Zulu	Hutchings <i>et al.</i> 1996
umagunda	Zulu	Von Breitenbach <i>et al.</i> 2001
uMagunda; uMaginda	Zulu	Palmer & Pitman 1972
umlahleni	Zulu	Cunningham 1988; Hutchings <i>et al.</i> 1996; Van Wyk <i>et al.</i> 1997; Von Breitenbach <i>et al.</i> 2001
umlahlenisefile; igejalibomvu; ijundumhlahleni	Zulu	Cunningham 1988; Hutchings <i>et al.</i> 1996
ugejelibomvu	Zulu	Ngwenya <i>et al.</i> 2003
Umgxcina	Zulu	Cunningham 1988
Umqxina	Zulu	Steedman 1933
inkunzitwalitshe; inphephelangen	Zulu	Hutchings <i>et al.</i> 1996
inPhephelelengi	Zulu	Cunningham 1988
umPhephelengi; umBese	Zulu	Palmer & Pitman 1972
om-Hlibe; um-Gxina; um-Guna; Moodalagweene	-	Burt Davy 1932

Van der Merwe 1309 (PRE). Van der Schijff 4642, 4675, 5121 (PRE). Van Son s.n. (PRE). Van Warmelo s.n. (PRE). Van Wyk 4110, 7005, 7528 (PRE). Van Wyk & Theron 4564 (PRE). B-E. & C.M. van Wyk 28 (JRAU). Van Wyk & Yembaturova 4218 (JRAU). Von Ludwig s.n. (STU)

Wager 23012 (PRE). Ward 3422 (PRE). Wells 2996 (PRE). West 3012, 3814 (PRE). Williams 2418 (NBG, PRE).

Zeyher 558, 7699 (PRE).

ACKNOWLEDGEMENTS

The authors offer their thanks to the University of Johannesburg and German Academic Exchange Service (DAAD) for funding the research. Also, we are much indebted to A.R. Magee (University of Johannesburg), Dr A.I. Konstantinova (Moscow State University), Dr A. Würz (STU), Anne Lise Fourie and Estelle Potgieter (both of the Mary Gunn Library, PRE) for valuable help during the preparation of the manuscript. We thank V. Papworth (BM) for kindly providing us with high resolu-

tion images of type specimens in the Banks Herbarium, and the curators and staff of PRE and NBG for allowing us to study their collections.

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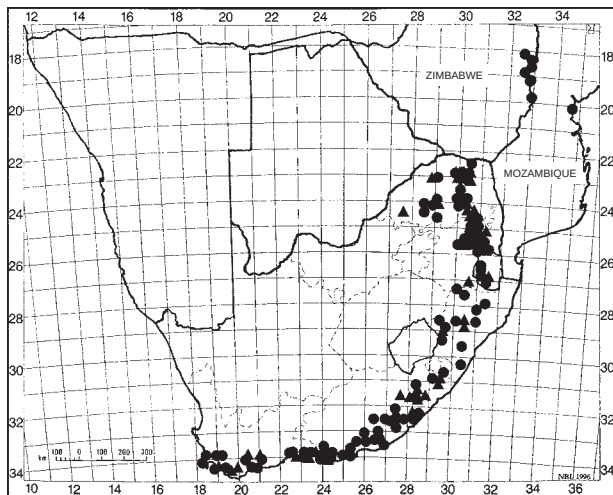


FIGURE 4.—Known distribution of *Curtisia dentata*, ●, in South Africa, Swaziland, Mozambique and Zimbabwe. Additional localities given by Von Breitenbach (1995), ▲.

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Notes on African plants

VARIOUS AUTHORS

CAMPANULACEAE

THEILERA ROBUSTA, THE CORRECT NAME FOR *THEILERA CAPENSIS*

When Hong (2003) described *Theilera capensis*, he overlooked important contributions to the taxonomy of the South African Campanulaceae, particularly that of Sonder (1865). In his epic work in *Flora capensis*, Sonder provided the first keys to species of *Lightfootia* and *Wahlenbergia*, described new species and made numerous new combinations. Among these was the transfer of *Lightfootia robusta*, a species described by De Candolle (1839), to *Wahlenbergia*. De Candolle based his name on a collection by Drège from Zwaanepoelportberg near Willowmore in the Eastern Cape. It would appear from the question mark after the generic name, that he was uncertain of the placement of this species. Additionally, Sonder reduced *Wahlenbergia rigida* Bernh. to synonymy under *W. robusta*. This species was described in 1844 based on a collection by Krauss from the Groot Winterhoekberge near Uitenhage in the Eastern Cape. In an unusual move, Kuntze (1891) transferred *W. robusta* (A.DC.) Sond. to *Campanopsis* R.Br., a name of different rank, regarded by him as having priority over *Wahlenbergia*.

Even after the account by Sonder, the identity of *Wahlenbergia robusta* remained confusing, and authentic material of the species appears unavailable. Von Brehmer (1915) omitted the species from his account of African *Wahlenbergia* and it is not clear what rationale he followed. When L. Bolus (1915) described *W. guthriei* from the southern Cape based on the description of Sonder, she suggested that this species is allied to *W. robusta*. According to her, the two species differ in leaf, calyx and corolla characters, with *W. guthriei* having ‘sessile leaves widened at the base and usually lobed, the corolla tube 2–3 times as long as the segments, and the calyx segments sometimes much longer than the valves of the capsule. The corolla is a deep blue and very fugitive’. Despite these differences pointed out by Bolus, many of the specimens of *W. guthriei* in BOL, NBG, PRE and SAM are labelled as *W. robusta*. Following the establishment of the segregate genus *Theilera* to accommodate *W. guthriei* (Phillips 1927), in herbarium practice *W. robusta* was often misidentified as *T. guthriei*. After visiting the National Herbarium (PRE) in South Africa, Hong (2003) described *T. capensis* based on unnamed specimens [Viviers & Vlok 181 (PRE), Acocks 16019 (PRE)] from Willowmore and Steytleville, respectively.

The search for the identity of *Wahlenbergia robusta* led to the examination of images of the type specimens of *Lightfootia robusta* (Drège 7691) and *W. rigida* (Krauss s.n.) from The Swedish Museum of Natural History and www.aluka.org, respectively. Unexpectedly these species resemble *Theilera capensis*. After examining the type specimen of *T. capensis* [Viviers & Vlok

181 (PRE)] I found all three types conspecific. Since *W. rigida* is a later name for *W. robusta*, the latter name has priority over *W. rigida* as required by Art. 11.4 of the Code (McNeill *et al.* 2006). The name *T. capensis* is therefore a synonym of *W. robusta*. Goldblatt & Manning (2000) argued for the return of *Theilera* to *Wahlenbergia*, whereas Hong (2003) stated that the two genera are distinct. Evidence from phylogenetic studies using morphology and DNA sequence data suggest that it is premature to return *Theilera* to *Wahlenbergia* (Cupido 2008) and that the two genera should be best kept separate for now. Despite the fact that *Theilera* is embedded among the *Wahlenbergia* species, the latter genus appears non-monophyletic. However, the results support the close affinity between the two species of *Theilera*. In view of the above discussion, the new combination *Theilera robusta* is here proposed as the correct name for *T. capensis*.

***Theilera robusta* (A.DC.) C.N.Cupido, comb. nov.**

Lightfootia robusta A.DC. in DC., Prodr. 7: 420 (1839). *Wahlenbergia robusta* (A.DC.) Sond.: 584 (1865). *Campanopsis robusta* (A.DC.) Kuntze: 379 (1891). Type: South Africa, Cape of Good Hope (Caput Bonae Spei), Drège 7691 (S, –photo!).

Wahlenbergia rigida Bernh.: 820 (1844). Type: South Africa, Uitenhage, Groot Winterhoekberg, Krauss s.n. (M, –photo!).

Theilera capensis D.-Y.Hong: 732 (2003). Type: South Africa, Cape Province, Solitree, Witteberg, peak north of farm ‘World View’, 1 200 m, 4 Jul. 1987, Viviers & Vlok 181 (PRE, holo!).

Additional specimens examined

Acocks 16019 PRE; Cupido 317 NBG; Long 1376 PRE; Taylor b PRE.

ACKNOWLEDGEMENTS

I wish to thank Prof. Thomas Lammers of the University of Wisconsin, Oshkosh for commenting on the first draft of this paper, and Dr Johannes Lundberg of The Swedish Museum of Natural History who kindly provided scanned images.

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MS. received: 2008-06-23.

ASPHODELACEAE: ALOOIDEAE

ALOE HAHNII, A NEW SPECIES IN THE SECTION *PICTAE*, IN THE SOUTPANSBERG CENTRE OF ENDEMISM, LIMPOPO PROVINCE, SOUTH AFRICA

The Soutpansberg Centre of Endemism is situated in the Limpopo Province and comprises the Soutpansberg and Blouberg Massifs. The highest point in the Soutpansberg is Lejuma at an altitude of 1 748 m, while the Blouberg rises to 2 051 m. The vegetation of the Soutpansberg is mainly bushveld and thicket, with Afro-montane forest patches on the south- and east-facing slopes. At higher altitudes, grasslands are found on particularly the southern slopes, and a fynbos-type vegetation grows in the mist belt at places along the summit. This centre of endemism shows clear floristic links with other Afro-montane areas such as the Wolkberg Centre to the south and the Chimanimani-Nyanga Centre in Zimbabwe to the north (Van Wyk & Smith 2001).

The Soutpansberg Centre harbours an estimated total of 3 000 vascular plant taxa of which ± 45 (1.5%) are endemic to the area. The genus *Aloe* L. is well represented in this centre of endemism. At least 13 *Aloe* taxa have been recorded along a 9 km transect from Hanglip in the south to Tshikuwi in the north (Van Wyk & Smith 2001).

There has long been doubt as to the exact identity of maculate aloes occurring in the Soutpansberg, previously identified as *Aloe swynnertonii* Rendle (= *A. chimanimaniensis* Christian) (Christian 1936). According to Carter (2001), *A. swynnertonii* only occurs in Montane grassland in the mountainous border between Zimbabwe and Mozambique, and the eastern outliers of these mountains. Carter (2001) further states that the disjunct population of *A. swynnertonii* near Lake Fundudzi in the Limpopo Province of South Africa, as reported by Christian (1936) and Reynolds (1950), probably represents an extreme form of a species from the Soutpansberg. The Lake Fundudzi plants have shorter bracts, pedicels and perianths than *A. swynnertonii* (Christian 1936; Reynolds 1950; Carter 2001).

The separate specific status of these plants was recently confirmed by Dr Norbert Hahn (pers. comm.). After extensive fieldwork in the Soutpansberg, he came to the conclusion that populations hitherto regarded as *A. maculata* All. from the Blouberg and Lejuma and *A. swynnertonii* from the eastern Soutpansberg (Hahn 2002, 2006) are the same taxon and represent extremes of a very polymorphic taxon. This taxon is considered to be endemic to the Soutpansberg region and is here described as *Aloe hahnii* Gideon F.Sm. & R.R.Klopper.

***Aloe hahnii* Gideon F.Sm. & R.R.Klopper**, sp. nov., a *A. swynnertonii* differt bracteis, pedicellis, perianthisque brevioribus et floribus nitidioribus scarlatinis magis decurvatisque.

TYPE.—Limpopo, 2230 (Musina): Soutpansberg, Lejuma, due E of Lejuma peak, (–AB), 2007-06-08, *Hahn 2172* (PRE, holo.), *Hahn 2171* (PRE, para.).

A. chimanimaniensis auct. sensu Christian: t. 639 (1936), p.p. quoad spec. et loc. reg. Transvaal; sensu Reynolds: 220 (1950), p.p. quoad spec. et loc. reg. Northern Transvaal.

A. maculata auct. sensu Hahn (2006), quoad loc. reg. Blouberg et Soutpansberg.

A. swynnertonii auct. sensu Glen & Hardy: 52 (2000), p.p. excl. ref. *A. petrophila* Pillans et *A. vogtsii* Reynolds; sensu Hahn (2006), quoad loc. reg. Soutpansberg.

Small, slow-growing, herbaceous, succulent, perennial herb, 200–400 mm tall, with rosettes solitary, not forming clusters, 250–400 mm diam. *Stems* usually absent, rarely up to 120 × 40–50 mm diam, creeping along ground, with persistent dried leaves. *Leaves* laxly rosulate, distinctly spreading, attenuate, tapering to dried, reflexed apex, 130–400 mm long, 40–60 mm broad at base, upper surface dull pale green to brown, with pale milky green to whitish spots, variously shaped and sized, sometimes $\pm$ confluent in transverse bands, densely dotted with tiny whitish dots, lower surface uniformly pale to milky green, with dense whitish to milky green spots, $\pm$ confluent in transverse bands, usually with longitudinal darker greenish or purplish striations; margin not distinctly coloured, with very pungent, straight, brownish orange teeth, 2–4 mm long, 7–14 mm apart, $\pm$ evenly spaced; leaf exudate drying opaquely yellow, cut end eventually turning dark purple. *Inflorescence* single, 260–1 000 mm tall, erect, 4–8(–10)-branched from above middle, upper branches rarely re-branched, branches erectly spreading. *Peduncle* 5–8 mm wide at base, matt purplish brown with a soft, whitish bloom, basally plano-convex; without sterile bracts; branches subtended by up to 30 mm long, 5–10 mm wide at base, straw-coloured, thin, scarious, many-nerved bracts. *Racemes* cylindrical to head-shaped, 40–60 × 50–70 mm, varying in size according to age of plants, larger in old plants, smaller in young plants, laxly flowered; buds erect to spreading, somewhat congested at apex, flowers subpendulous when open. *Floral bracts* amplexicaul, 5–15 × 2–3 mm, dirty brownish white, margins the same colour, thin, scarious, many-

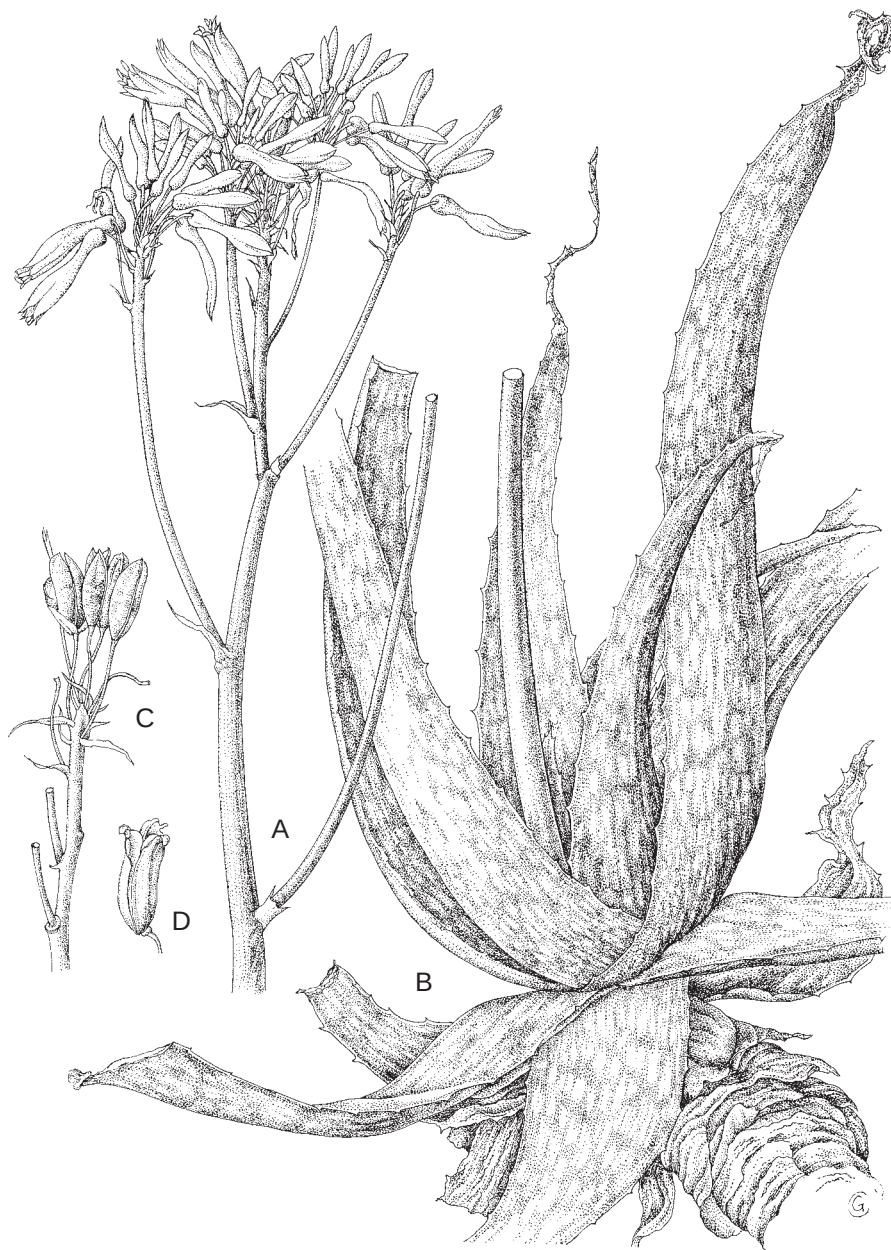


FIGURE 1.—*Aloe hahnii*, Smith & Klopper 1. A, inflorescence, $\times 0.6$; B, plant, $\times 0.6$; C, infructescence, $\times 0.6$; D, fruit capsule, $\times 0.6$. Artist: G. Condy.

nerved. *Pedicels* 10–20 mm long, red. *Flowers*: perianth varying from uniformly red to tri-coloured with green, creamy white and reddish tips, 25–28 mm long, 5–7 mm across ovary, abruptly constricted to 3–4 mm above ovary to form basal swelling, widening towards middle to 5 mm, widening towards throat and wide open mouth, cylindric-trigonal; outer segments free for 12–14 mm, tips recurved and slightly spreading. *Stamens* with slightly flattened, pale lemon-yellow filaments, hardly exserted. *Ovary* 5–6 $\times$ 2 mm, bright light green; style not exserted. *Fruit* cylindric-oblong, matt light green capsule, 20–25 $\times$ 7–10 mm. *Seed* not seen. *Flowering time*: June to July. *Chromosome number*: unknown. Figure 1.

Habitat: *Aloe hahnii* occurs in the mist belt regions of the Blouberg and most of the Soutpansberg in Soutpansberg Arid Mountain Bushveld (Mucina & Rutherford 2007). The altitude ranges from 1 000 m in Venda to 2 050 m on the Blouberg. It commonly grows on sandy soil derived from the Soutpansberg Group Quartzites (Barker *et al.* 2006). This aloe has been found in *Coleochloa set-*

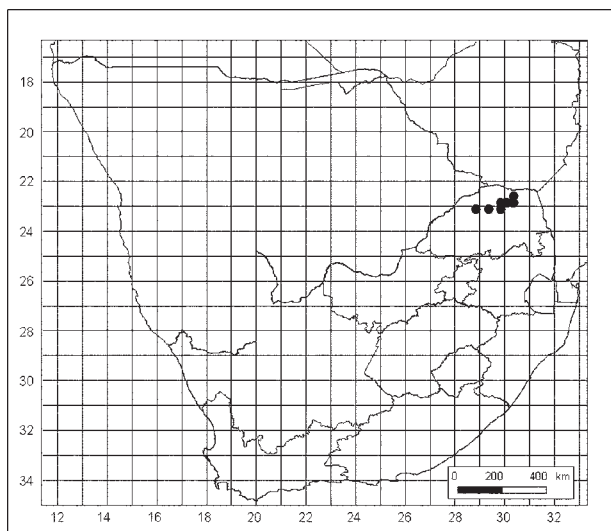
ifera-dominated grassland up to the margins of forests on the Blouberg and similar vegetation on the Soutpansberg, whereas in the western Soutpansberg it sometimes grows in low closed woodland in full shade (N. Hahn pers. comm).

Illustration: Smith & Van Wyk: 48 (2008).

Distribution: this aloe occurs on the Blouberg and Soutpansberg massifs in the Limpopo Province of South Africa (Figure 2).

Etymology: the taxon is named for Dr Norbert Hahn, expert on the flora of the Soutpansberg.

Diagnostic characters: *Aloe hahnii* differs from *A. swynnertonii* in the shorter bracts, pedicels and perianths, as well as flowers that are a glossier scarlet-red and more decurved. It is distinguished from *A. vogtsii* Reynolds, with which it occasionally grows sympatrically in the central regions of the Soutpansberg mist belt, by the latter species having buds that are borne horizontally in more elongated (not capitate) racemes (Table 1).

FIGURE 2.—Distribution of *Aloe hahnii*.

Other specimens examined

LIMPOPO.—2229 (Waterpoort): Louis Trichardt, Hanglip, (–DD), Rossouw 131 (PRE); Louis Trichardt, Plaas Beeston, ± 17 km from Louis Trichardt-Messina road, on Bluegum road, (–DD), Rossouw 170 (PRE). 2230 (Musina) [Messina]: Dzanani, (–CB), Hahn 534 (PRE); Thohoyandou, between Mohepu Resort and Khakhu, (–CC), Grace, Van Wyk, Nkuna & Mabatha 59 (PRE); Khaku, (–CC), Hahn 2173 (PRE); Thohoyandou, Vhufuli, NE of Donald Frasers, (–CD), Hahn 127 (PRE); Thate Vondo, (–CD), Hahn 2176 (PRE); Sibasa, Lake Fundudzi, mountain slopes, (–CD), Hardy & Van Graan 3687A&B (PRE); Sibasa Dist., Tate Vondo Forest Reserve, (–CD), Hemm 119 (PRE); Sibasa, Lake Fundudzi, (–CD), Reynolds 1873 (PRE); Zoutpansberg Dist., Sibasa, 10 miles [16 km] W of Sibasa and about 30 miles [48 km] NE of Wyliespoort, (–CD), Reynolds 2501 (PRE); Lake Fundudzi, (–CD), Reynolds PRE38019 (PRE); Venda, Tate Vondo, (–CD), Van Wyk 5572 (PRE); Zoutpansberg Dist., Lake Fundudzi, (–CD), Vogts & Galpin PRE21202 (PRE). 2328 (Baltimore): Blouberg Nature Reserve, Ga-Monnaasemoriri, kloof E of mountain on cliffs, (–BB), Archer 535 (PRE); Soutpansberg Dist., Blaauwberg, (–BB), Meeuse 10343, Van der Merwe 1362 (PRE); Pietersburg Dist., Blaauwberg, top near beacon, (–BB), Strey & Schlienben 8536 (PRE). 2329 (Polokwane): Soutpansberg, Lejuma, 500 m W of home, (–AB), Hahn 2168, 2169 (PRE); Soutpansberg, Lejuma, Smith & Kloppe 1 (PRE); Soutpansberg, Llewelly 35 LS, hill on W boundary leading to high point, (–AB), Venter 6174 (PRE); Soutpansberg Dist., Louis Trichardt, summit of Hanglip peak, (–BB), Galpin 9681 (PRE).

ACKNOWLEDGEMENTS

The authors would like to thank the following people: Dr Norbert Hahn for providing the authors with addi-

TABLE 1.—Differences between *Aloe hahnii* and *A. swynnertonii*

	<i>A. hahnii</i>	<i>A. swynnertonii</i>
Bract length (mm)	5–15	8–20
Pedicle length (mm)	10–20	20–35
Perianth length (mm)	25–28	25–35
Flower colour	Glossy scarlet-red	Orange-red to pinkish red
Flower shape	Decurved	Slightly curved

tional material and information regarding this new aloe; Ms Hester Steyn, Data Management Unit, SANBI, Pretoria, for producing the distribution map; Dr Otto Leistner for providing the Latin diagnosis; Ms Gill Condry for the line drawing; two referees for suggesting improvements to the manuscript.

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MS. received: 2008-09-04.

ASPHODELACEAE: ALOOIDEAE

FORMALIZING THE SYNONYMY OF *BULBINE TRIEBNERI*

Kloppe *et al.* (2008) reported on the conspecific status of *Bulbine triebneri* Dinter and *B. alba* Van Jaarsv., but neglected to formalize the synonymy of the later name under the earlier name, which takes priority under the rules of the International Code of Botanical Nomenclature (McNeill *et al.* 2006). This is now done here:

***Bulbine triebneri* Dinter** in Poelln., Feddes Repertorium 52: 113 (1943). *Bulbine frutescens* (L.) Willd. var.

triebneri (Dinter) Baijnath: 348 (1977). Type: Namibia, 2818 (Onseepkans): Great Namaqualand, Endoorn, east of Warmbath, (–DA), Dinter 7899 (B, lecto.!–K, photo.).

Bulbine alba Van Jaarsv.: 37, 39 (2001). Type: Western Cape, 3221 (Ladismith): Little Karoo, Ockertskraal, shale ridge amongst loose fragments, (–CD), 1998, U. de Villiers Pienaar s.n. (NBG, holotype!).

It is important to note that *Bulbine alba* is not considered to be a nomenclaturally superfluous name, as Van

Jaarsveld (2001) did not include the type of *B. triebneri* in the circumscription of his taxon.

ACKNOWLEDGEMENTS

We would like to thank Dr Dee Snijman from the Compton Herbarium for bringing the omission in the previous report to our attention and also Dr Hugh Glen from the KwaZulu-Natal Herbarium for his input and discussions about citing synonymy and the ICBN.

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MS. received: 2008-08-13.

EBENACEAE

TIPIFICATION AND A NEW STATUS IN *DIOSPYROS*

INTRODUCTION

Maba natalensis, the basionym of *Diospyros natalensis*, was published by Harvey (1863) and based on a Gerard & McKen specimen from Durban, KwaZulu-Natal. For a long time this species was known as a constituent of coastal dune forest ranging from East London to northern KwaZulu-Natal. Hutchinson (1912) described *M. dawei* from Mozambique, but it was subsequently transferred to *Diospyros* by Brenan (1948) as *D. dawei*, a taxon which turned out to be a small leaf form of *D. natalensis*, and the latter's distribution range was consequently extended along the coast through Mozambique and Tanzania to as far north as southern Kenya.

Brenan (1948) described a related species, *Diospyros nummularia* from Zimbabwe, based on a specimen collected by Eyles in the present-day Harare, Zimbabwe. For a long time it was thought that this species was confined to granite outcrops near water in Zimbabwe, but it was also found in the Crocodile Gorge, Mpumalanga, and on the Lebombo Mountains in Swaziland and adjacent parts of Mozambique. Brenan (1954) added a third species to this complex, *D. nyasae* from Malawi. It was first collected on Mt Mulanje (formerly Mt Mlanje) in 1946 by L.J. Brass and he recorded this plant as growing on the flood-swept edges along the Likabula River, a habitat which prompted Van Steenis (1981: 225) to list the species as a rheophyte. With leaves long and narrow, tapering at both ends and usually 32–41(–50) mm long, *D. nyasae* has been referred to by various authors (White 1983, 1988; White & Verdcourt 1996) as the 'stenophyllous or narrow-leaved form' or 'Mulanje variant' of *D. natalensis*.

Diospyros natalensis varies considerably in leaf shape and size (White 1988: fig. 10). *D. nyasae* and the much smaller rounded-leaved form, *D. nummularia*, are merely two extreme forms at opposite ends of the range of leaf variation in the *D. natalensis* complex. *D. num-*

mularia has consistently small, roundish leaves and is confined to riverine forest, usually among granitic boulders, or seasonal streams or riverbeds in *Brachystegia* woodland; both habitats are occasionally subjected to flooding. *D. nyasae*, on the other hand, still fits into the wider concept of the variable *D. natalensis*, and many intermediates are known from Mt Mulanje where this form was first described. Therefore I agree with White in Van Steenis (1981: 225) that these intermediate specimens (*Brass* 16385, *Buchanan* 975, *Chapman & Chapman* 7065, 8138, *Graham* 2170 and *Muller* 1581) cannot even be recognized as a subspecies (although it may well be a subspecies 'in the making'), and it is therefore considered conspecific with *D. natalensis*.

Diospyros natalensis, as defined here in a broad sense, is associated with forest and usually grows near or in water along stream or river banks, occasionally on coastal dunes or along the shores of fresh water lakes (De Winter 1963). *Diospyros natalensis* and *D. nummularia* are obviously very closely related. The flowers are similar and both have acorn-shaped fruit with a sharp tip at the apex, clasped by a slightly accrescent calyx at the base (thus resembling an acorn), but the two taxa can be separated on vegetative characters and geographical distribution. Therefore, to acknowledge these differences, the two taxa are here considered subspecies of *D. natalensis*, rather than one variable species as treated by White (1983, 1988) and White & Verdcourt (1996).

De Winter (1963) recognized *Diospyros natalensis* and *D. nummularia* as two distinct species, but noted that *D. nummularia* may prove to be only a subspecies of *D. natalensis*. White (1988) stated that *D. natalensis*, *D. nummularia* and *D. nyasae* were connected by intermediates and therefore he recognized only one variable species, namely *D. natalensis*. White must, however, have changed his mind at some stage, because there are some earlier annotated specimens with White's determinative labels, dated 1968, containing the manuscript

names *D. natalensis* subsp. *natalensis* (Buchanan 975 at Kew and type of *D. nyassae*) and *D. natalensis* subsp. *nummularia* (Eyles 3414 at Kew and type of *D. nummularia*). Subsequently, some authors (e.g. Palmer & Pitman 1973; Coates Palgrave 1977; Pooley 1993; McClelland 2002) cited *D. nummularia* as a subspecies of *D. natalensis* in error, assuming that White had validly published this infraspecific name. None of these authors cited the basionym and according to Article 33.4 of the International Code of Botanical Nomenclature (McNeill *et al.* 2006), the name *D. natalensis* subsp. *nummularia* is therefore not validly published. The new combination is made in this paper. *D. nyassae* is a synonym of *D. natalensis* subsp. *natalensis* (White 1983).

Linnaeus (1753) described *Royena lucida*. When southern African species of *Royena* were transferred to the genus *Diospyros* (De Winter & White 1961), the specific epithet *lucida* could not be used because the name *D. lucida* (Loudon 1841) already existed for another taxon and such a combination would have been considered a later homonym. The next available epithet was *whyteana* from the basionym *Royena whyteana* described by Hiern (1894) from a specimen collected by Alexander Whyte (1834–1908) on Mt Mulanje, Malawi. Today, only a fragment of the holotype exists in the British Natural History Museum, London (BM). Although it is a sterile specimen with only a few leaves and without any flowers or fruit, it cannot easily be mistaken for any other *Diospyros* species growing on Mt Mulanje. It is not considered an ambiguous specimen and therefore there is no need to appoint an epitype. The fruit of *D. whyteana* is very distinctive with the inflated accrescent calyx that envelops the fruit completely. Chapman recollected herbarium material at the type locality in 1957, and the Kew specimen (Chapman 247) is cited in *Flora zambesiaca* by White (1983) and a duplicate is housed in PRE. This confirms the existence of *D. whyteana* on Mount Mulanje.

Gürke described *Royena wilmsii* in 1898, based on a Wilms specimen, and *R. goetzei* and *R. nyassae* in 1901, based on Goetze specimens housed in the Berlin Herbarium. All three of these taxa are conspecific with *Diospyros whyteana* (De Winter 1963). In the case of the holotypes (Wilms and Goetze specimens), which were destroyed in the Berlin Herbarium during World War II, lectotypification is covered by Article 9.15 of the Code (McNeill *et al.* 2006), which provides for the restriction of the lectotype to a single specimen. The Aluka Library (<http://www.aluka.org/>) indicates that adequate duplicate herbarium material of Goetze has survived in the National Botanic Garden of Belgium in Meise (BR), sufficing as lectotypes for *R. goetzei* and *R. nyassae*. In the case of *R. wilmsii*, an isotype survived in Kew and it is here selected as the lectotype.

TAXONOMY

Specimens seen on the Aluka Library website (<http://www.aluka.org/>) are distinguished by the code e! in the citations.

1. ***Diospyros natalensis* (Harv.) Brenan** in Memoirs of the New York Botanic Gardens 8,5: 501 (1954); De

Winter: 58 (1963); R.B.Drumm.: 267 (1975); F.White: 254 (1983); F.White: 343 (1988); Pooley: 404 (1993); F.White & Verdc.: 13 (1996); M.Coates Palgrave: 905 (2002). Type: South Africa, KwaZulu-Natal, Durban, Gerrard & McKen 675 (TCD, holo. e!; K, iso. e!).

Maba natalensis Harv.: 7 (1863); Hiern: 131 (1873).

Maba dawei Hutch.: 330 (1912). *Diospyros dawei* (Hutch.) Brenan: 111 (1948). Type: Mozambique, Chimoio, Garuso, Dawe 524 (K, holo. e!).

Diospyros nyassae Brenan: 500 (1954). Type: Malawi, without precise locality, Buchanan 957 (K, holo. e!).

Evergreen, multistemmed, much-branched shrub or small tree up to 6 m tall. Branches with widely spaced, white lenticels. Leaves simple, alternate, dark glossy green above, paler below; lamina with numerous small black dots and sometimes with larger black ones that might serve as extrafloral nectaries. Flowers white, small, up to 5 mm long. Corolla deeply 3-lobed, densely silvery hairy outside, with reflexed lobes; male flowers solitary or in clusters; female flowers solitary in axils of leaves. Fruit an acorn-shaped berry, $\pm 12 \times 6$ mm, with short sharp tip, seated in cup-shaped persistent calyx, orange to red when mature.

Key to subspecies of *Diospyros natalensis*

- 1a Young branches and petioles with long spreading hairs mixed with short, stiff hairs; leaves ovate or narrowly elliptic, usually > 15 mm long and wider than 10 mm; midrib distinct from base to apex on both lamina surfaces; lamina margin usually with long spreading hairs; pedicels with few hairs or glabrous *D. natalensis* subsp. *natalensis*
- 1b Young branches and petioles densely covered with short, stiff hairs only, without long spreading hairs intermixed; leaves orbicular or suborbicular, < 15 mm long and narrower than 13 mm; midrib widened near base, distinctly sunken above for most of its length, disappearing before reaching apex (Figure 3), distinct along entire length on lower lamina surface; lamina margin without long spreading hairs; pedicels puberulous *D. natalensis* subsp. *nummularia*

1a. subsp. *natalensis*

Diagnostic characters: leaves are ovate or narrowly elliptic, 15–25(–50) $\times$ 10–15(–25) mm, dark glossy green above or with a whitish bloom and much paler below. Petioles are sometimes glabrous for example in specimens from Mt Mulanje (Malawi). For additional diagnostic characters see key above.

Distribution and habitat: subsp. *natalensis* occurs in the coastal regions of southern Kenya, Tanzania, Mozambique, and in South Africa in KwaZulu-Natal and Eastern Cape as far south as East London. Its distribution extends inland into Malawi to Mt Mulanje near the border with Mozambique and the most eastern parts of Zimbabwe. Specimens inland from Lake Tanganyika [Lake Nyasa], Democratic Republic of Congo, northern Zambia and Lake Mweru, also seem to belong to subsp. *natalensis* (Figure 4). It is associated with forest on coastal dunes, along streams and rivers or the edges of lake shores.

1b. ***Diospyros natalensis* (Harv.) Brenan** subsp. ***nummularia* (Brenan) Jordaan**, stat. nov.

Diospyros nummularia Brenan in Kew Bulletin 1948: 111 (1948); De Winter: 58 (1963); M.Coates Palgrave: 906 (2002). Type: Zimbabwe, Harare [Salisbury], Eyles 3414 (K, holo. e!).



FIGURE 3.—Leaves of *Diospyros natalensis* subsp. *nummularia*: midrib disappears before it reaches apex on upper surface.

Diagnostic character: the leaves are orbicular or sub-orbicular, 6–12(–15) × 7–10(–13) mm, very dark glossy green above, much paler below. For additional diagnostic characters see key above.

Distribution: subsp. *nummularia* occurs in southern Malawi, Zimbabwe, Mozambique (Tete Province), at Cahora Bassa, Mpumalanga in South Africa, and in Swaziland, especially along the Lebombo Range (Figure 4). It grows between granite rocks in streambeds fringed by riverine forests.

2. *Diospyros whyteana* (Hiern) F.White in Bothalia 7: 458 (1961); F.White: 326 (1962); De Winter: 69 (1963); F.White: 94 (1971); R.B.Drumm.: 267 (1975); F.White: 269 (1983); Pooley: 406 (1993); F.White & Verdc.: 28 (1996); A.E.van Wyk & P.van Wyk: 184 (1997); McClelland: 518 (2002); M.Coates Palgrave: 911 (2002). Type: Malawi, Mlanje [Mulanje], *Whyte s.n.* (BM, fragment, holo. e!).

Royena whyteana Hiern: 25 (1894). *R. lucida* L. var. *whyteana* (Hiern) De Winter & Brenan: 499 (1954).

R. lucida L.: 397 (1753) non *Diospyros lucida* Hort. ex Loudon: 394 (1841); Hiern: 447 (1906). Type: South Africa, locality unknown, *Linnaean Herbarium* No. 570.1 [LINN, lecto., designated by White & Verdcourt (1996)].

R. wilmsii Gürke: 60 (1898). Type: South Africa, Gauteng, Pretoria, *Wilms* 923 (B, holo.†; K000350826, lecto. e!, designated here).

R. goetzei Gürke: 372 (1901). Type: Tanzania, Mbeya Dist., Igala Pass, *Goetze* 1344 (B, holo.†; BR, lecto. e!, designated here; BM, isolecto.).

R. nyassae Gürke: 373 (1901). Type: Tanzania, Kingagebirge, *Goetze* 1203 (B, holo.†; BR, lecto. e!, designated here; BM, isolecto.).

ACKNOWLEDGEMENTS

The author is greatly indebted to the reviewers for constructive comments on the manuscript and to Hester Steyn for preparing the distribution map.

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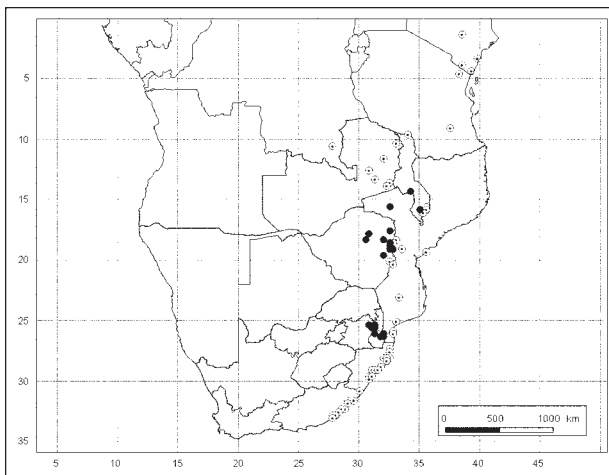


FIGURE 4.—Known distribution of *Diospyros natalensis* subsp. *natalensis*, ○; and *D. natalensis* subsp. *nummularia*, ●, based on specimens in the National Herbarium, Pretoria (PRE).

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MS received: 2008-07-07.

THYMELAEACEAE

THE TRUE IDENTITY OF *SYNAPTOLEPIS KIRKII*

INTRODUCTION

Synaptolepis kirkii was originally described by Oliver (1870) in *Hooker's Icones Plantarum* 11, and the type locality of *Kirk* 37 given as Zanzibar. Subsequently, *S. oliveriana* was described by Gilg (1894a) from a specimen, *Monteiro* 45, collected in Delagoa Bay [Maputo] in Mozambique in 1876. In a second publication in the same year, Gilg (1894b) does not mention *S. oliveriana*, but the illustration of the flowers (fig. 81), represents *S. oliveriana*. Peterson (1959) in his revision of *Synaptolepis* in Mozambique recognizes *S. oliveriana* and refers to *S. kirkii* as occurring in Tanzania.

Peterson (1978) mentions under the distribution of *Synaptolepis kirkii*, that besides occurring in Kenya and Tanzania, it also occurs in Mozambique and South Africa (Natal). Bredenkamp & Beyers (2003) and Bredenkamp (2006) also mention *S. kirkii* occurring in South Africa. However, Peterson & Verdcourt (2006) bring clarity to this taxonomic confusion by stating that all the Mozambique material referred to in the above-mentioned publications, has proved to be *S. oliveriana*. *S. oliveriana* grows in sand forest or thicket on coastal dunes in sandy soil at low altitudes in the far northern parts of KwaZulu-Natal and Mozambique, mainly in the Maputaland Centre of Endemism (Van Wyk & Smith 2001). In Mozambique it occurs in Maputo, on the Inhaca and Bazaruto Islands, Xai-Xai and as far north as Quelimane, Pemba and Moçimboa da Praia, north of the Zambezi River.

A third species, *Synaptolepis alternifolia* Oliv. (including *S. longiflora* Gilg) occurs in Zimbabwe, Malawi, central and northern Mozambique and Tanzania. It differs mainly from *S. kirkii* and *S. oliveriana* by its terminal, 3–10-flowered cymose inflorescences. The first-mentioned

species has inflorescences comprising axillary, solitary flowers or flowers in 2–4-flowered axillary fascicles. *Synaptolepis* therefore comprises five species on the African continent (two more in West Africa and Sudan) and one species in Madagascar (Herber 2003; Peterson & Verdcourt 2006; Mabberley 2008).

Therefore, *S. kirkii* is considered as a misapplied name in the FSA region and only occurs along the coast of Somalia (Thulin 2006), Kenya and Tanzania, including the island of Zanzibar.

DIAGNOSTIC CHARACTERS

Distinctive characters among members of the genus are the transversely elongated lenticels of older stems that become wart-like (Figure 5A) and the pedicels are sometimes glandular (Figure 5B). These characters are present in all three southern and tropical African species which are very closely related. However, the main morphological differences between *Synaptolepis kirkii*, *S. oliveriana* and *S. alternifolia* are given in Table 2 and a key is provided.

Key to species of *Synaptolepis*

- 1a Leaves usually shorter than 24 mm; South Africa and Mozambique *S. oliveriana*
- 1b Leaves usually longer than 24 mm:
 - 2a Inflorescences axillary, solitary or few-flowered fascicles; petals comprise lobed ring without hairs; Somalia, Kenya and Tanzania *S. kirkii*
 - 2b Inflorescences terminal, 3–10-flowered cymes; petals comprise lobed ring with stiff white hairs; Zimbabwe, Malawi, Mozambique, Tanzania *S. alternifolia*

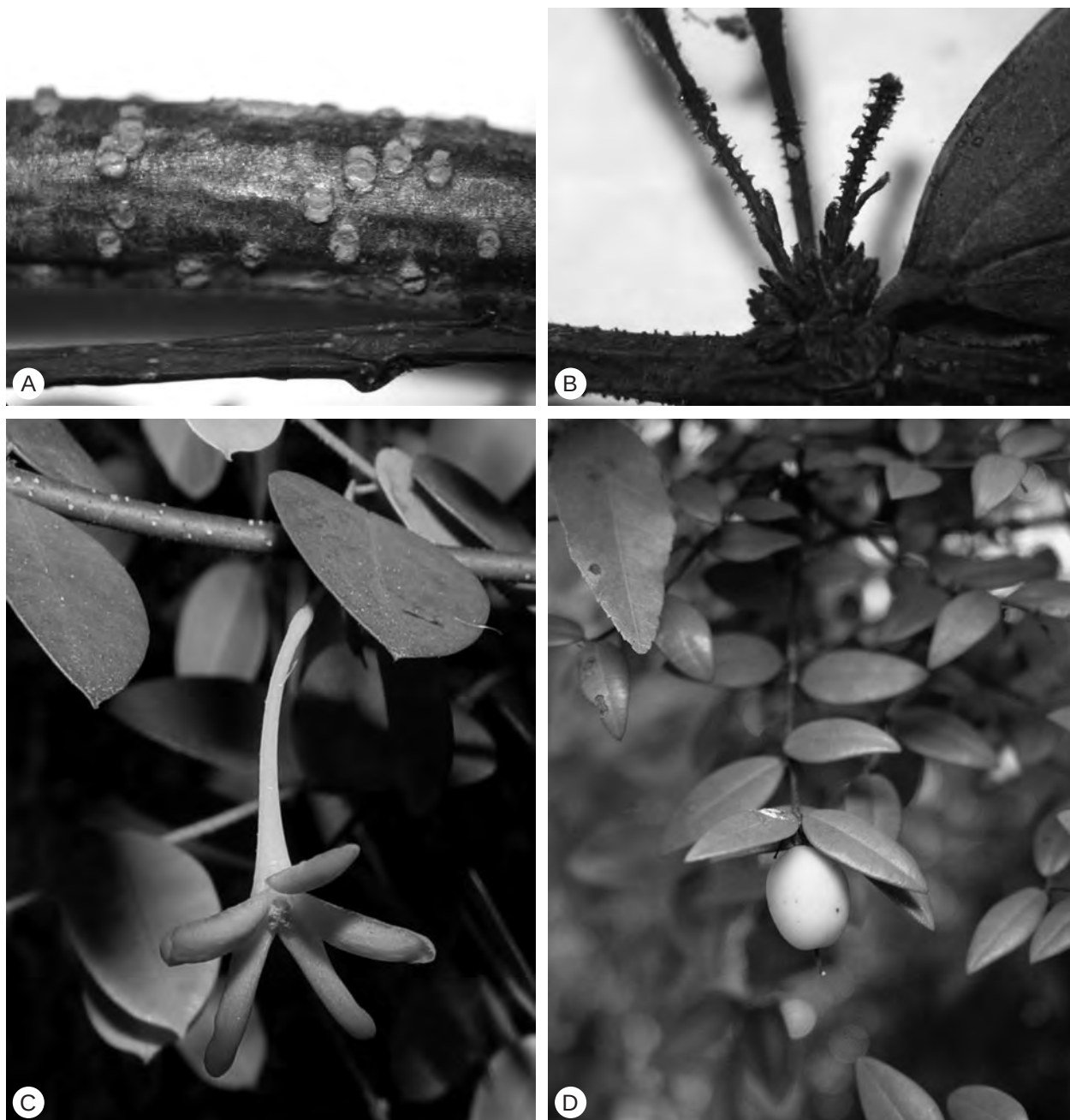


FIGURE 5.—*Synaptolepis*. A, transversely elongated lenticels of older stems; B, glandular pedicels. C, D, *Synaptolepis oliveriana*: C, flower; D, fruit. Photographers: A, B, M. Jordaan; C, D, G. Nichols.

TAXONOMY

Specimens seen on the Aluka Library website, <http://www.aluka.org/> are distinguished by the code e! in the citations. For flowers and fruits see Figure 5C, D.

***Synaptolepis oliveriana* Gilg** in Botanische Jahrbücher 19: 276 (1894a); Gilg: 231, fig. 81 F–J (1894b); C.H.Wr.: 80 (1915); B.Peterson: 218 (1959); B.Peterson & Verdc.: 87 (2006). Type: Mozambique, Delagoa Bay [Maputo], *Monteiro* 45 [B, holo.†; K, lecto. e!, designated by Peterson & Verdcourt (2006); P, isolecto. e!].

S. kirkii sensu C.H.Wright: 80 (1915) quoad *Bolus* 9762.

Erect, straggling or scrambling shrub up to 1 m high or a woody climber up to 3 m, occasionally up to 5 m tall, much-branched; branches divaricate, longitudinally

ribbed, brown or blackish, hairless, young branches sometimes glandular, covered with numerous rounded lenticels, becoming horizontally elongated, very prominent and wart-like on older stems (Figure 5A). Bark dark brown, rough, flaky, fibrous. *Stipules* lanceolate, 1.0–1.5 mm long; margin ciliate. *Leaves* simple, opposite or subopposite, leathery, dark glossy green above, paler below, hairless, bundles of fibrous vessels in blade visible when torn apart, especially along midrib; lamina elliptic or ovate, 8–20(–24) × 5–15(–17) mm, apex obtuse, acute or abruptly acuminate, base cuneate, rounded to truncate, margin entire, thickened; midrib sunken above, prominently raised below, with parallel lateral veins running straight into margin or disappearing before reaching margin, inconspicuous above, prominent below, reticulate venation obscure; petiole 1–2 mm long, transversely wrinkled and grooved above. *Inflor-*

TABLE 2.—Main differences between *Synaptolepis kirkii*, *S. oliveriana* and *S. alternifolia*

	<i>S. kirkii</i>	<i>S. oliveriana</i>	<i>S. alternifolia</i>
Distribution	Kenya, Somalia, Tanzania	Mozambique, South Africa (KwaZulu-Natal)	Malawi, Mozambique, Tanzania, Zimbabwe
Habitat	Miombo woodland and riverine forest	Sand forest, coastal dunes or thicket	Miombo woodland, riverine and sand forest
Habit	Usually woody climber or scrambling shrub	Small shrub in open grassland or disturbed areas, in forest, terminal twigs twining in vegetation	Shrub or woody climber
Young branches	Glandular, often with short, stiff hairs	Glabrous or glandular, rarely with short, stiff hairs	Glabrous or often with few long white hairs
Leaves	Broadly ovate, usually longer than 24 mm	Elliptic to broadly elliptic, or ovate, usually shorter than 24 mm	Elliptic, usually longer than 24 mm, sometimes shorter
Inflorescence	Axillary, solitary or few-flowered fascicles	Axillary, solitary or in pairs	Terminal, 3–10-flowered cymes
Pedice	Glandular	Often glandular	Usually glabrous, sometimes with few long white hairs, occasionally glandular
Pedice length from 2nd bract to base of hypanthium	5–6 mm	3.0–4.5 mm	3.5–6.0 mm
Hypanthium	Hairy or glabrous on outer surface	Glabrous on outer surface	Glabrous on outer surface
Petals	Lobed ring without hairs	Lobed ring with ciliate margins	Lobed ring with stiff white hairs

escence axillary, of solitary or paired flowers; bracts with ciliate margins, 1–2 mm long. *Flowers* white, sweetly scented (Figure 5C); pedicels $\pm$ 3–4 mm long, often glandular (Figure 5B). *Hypanthium* funnel-shaped, 10–15(–19) mm long, hairless on outer surface; lobes elliptic, 3.5–5.0 $\times$ 1.0–2.0 mm, apex obtuse, hairless. *Petals* forming a ring with membranous lobes, margin ciliate. *Stamens* 10, in 2 whorls in throat of calyx, included. *Disc* cup-shaped with small lobes, $\pm$ 0.5 mm long. *Ovary* ovoid, sessile, hairless. *Fruit* a drupe, oblong-ellipsoid, $\pm$ 12 $\times$ 10 mm, enclosed in persistent, $\pm$ fleshy base of hypanthium, yellowish to orange, turning blackish, smooth (Figure 5D).

Selected specimens examined

MOZAMBIQUE.—1140 (Moçimboa da Praia): Cabo Delgado Prov., Moçimboa da Praia, (–AD), *Mendes* 151 (PRE). 1340 (Pemba): Porto Amelia [Pemba], (–BA), *Gerstner* 7171 (PRE). 1737 (Quelimane): Zambezia, 20 miles [32 km] N of Quelimane, (–CA), *Wild* 5870 (PRE, SRGH). 2135 (Bazaruto Island): Bazaruto Island, (–CB), *Mogg* 28625 (PRE). 2434 (Chidenguele): Chidenguele [Chidenguel], (–CC), *Pedro & Pedrogar* 1806 (PRE). 2435 (Nhacoongo): Sul do Save Prov., Nhacoongo [Inhacoongo], (–AC), *Macedo & Balsinhas* 1102 (PRE). 2532 (Maputo): Maputo [Lourenço Marques], (–DC), *Borle* 158, 181 (PRE); Rikatla [Ricatlá], (–DC), *Junod TVM20144* (PRE). 2533 (Xai-Xai): Gazaland, Masiyena [Masiyani], mouth of Limpopo River, (–AB), *Earthy* 87 (PRE). 2632 (Bela Vista): Inhaca Island, (–BB), *Mogg* 27211, 27624, 27645, 27521, 28308 (PRE).

KWAZULU-NATAL.—2632 (Bela Vista): Maputaland, Tembe-Nduma corridor, (–CD), *Burrows* 7015 (PRE); 5 miles [8 km] NE of Makanes Drift, (–CD), *Ross* 2366 (NH, PRE); Makanes drift, 3 miles [4.8 km] S of drift in sand forest, (–CD), *Ross & Moll* 1809 (PRE); Kosi Bay, at NW side of Lake Nhlanga, (–DD), *Venter* 11,536 (PRE); Kosi, Sifungo, NW of Sifungo, (–DD), *Ward* 8473 (PRE). 2732 (Ubombo): Ingwavuma Dist., Lake Vasi, (–BA), *Vahrmeijer* 1109 (PRE); Maputaland, Sileza, (–BA), *Williams* 968 (NH, PRE); Mbazwana Forest Reserve, Mobola veld, (–BC), *Gerstner* 4808 (PRE); Sibayi area, between Sordwana Bay and Jozini, (–BC), *Van der Schijff* 6585 (PRE); Ubombo Dist., near Manzengwenya Inspection Quarters, (–BD), *Moll* 4862 (PRE); Hlabisa Dist., False Bay Park, (–CD), *Gerstner* 5068 (PRE); Ubombo Dist., Mpangazi, (–DA), *Strey* 5088 (PRE). 2832 (Mtubatuba): Nyalazi State Forest, Kentron area, (–AB), *Nicholas* 1598 (PRE); Hlabisa Dist., E of Nyalazi River, (–AB), *Ward* 3042 (PRE); St Lucia System, Bhangazi Lake, (–BA), *Ward* 9502 (PRE).

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MS. received: 2008-08-19.

Closing bodies in the capsular fruits of Ruschioideae (Aizoaceae)—a review

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Keywords: Aizoaceae, capsular fruits, closing bodies, hygrochasy, Mesembryanthema

ABSTRACT

Capsular fruits of the Mesembryanthema* are uniquely diverse and have been used to establish groupings within the tribe Ruschieae. The function, structure and development of the closing bodies of the Ruschioideae are reviewed from existing literature and are supplemented by personal observations, providing a framework for future research aimed at resolving critical issues regarding the structure and taxonomic implications of the closing bodies of the Ruschioideae. The number of species per taxon, distribution and presence or absence of covering membranes and closing bodies within the Mesembryanthema are tabulated.

INTRODUCTION

In the past, the structure of the capsular fruits was considered critical in the systematics of the Mesembryanthema (Herre 1971; Hartmann 1988, 1991, 1993, 2001; Smith *et al.* 1998). In particular, it is the internal structure of the capsular fruits that yields most of the variable characters. However, with the publication of molecular data by Klak *et al.* (2003, 2007) it was found that the groupings proposed by Hartmann were not supported by molecular data.

In many Mesembryanthema the locules are covered by roof-like lids known as covering membranes, leaving only a narrow distal opening through which seeds can be dispersed. This entrance is frequently closed to some degree and the blockage has an immensely important role in the dissemination biology of the Mesembryanthema as it results in the complete or partial occlusion of the locule. Seeds are consequently locked in and cannot simply be washed out by raindrops as in other species that lack such blocking devices. This structure results in the seeds being forced out, jet-like, through the gaps between the covering membranes (Parolin 2006).

The distal closing devices are generally very diverse in their structure, but two main types are distinguished. By far the most striking are the closing bodies, which are prominent and often hemispherical structures formed on the fruit wall near the upper end of the placentas (Figure 1A). The second type of closing device (Figure 1B), in the form of bulges, ledges and rodlets (Hartmann 1991), occurs on the lower surface of the covering membrane near the distal end. In a number of species, none of these closing devices are present, but dense bundles of funi-

cles sometimes close the locule entrance to a certain extent (Figure 1C; *Lampranthus* Group, Hartmann 1988, 1991; some *Drosanthemum* species, Hartmann & Bruckmann 2000; *Hereroa*, Dehn 1992). In some Mesembryanthema, the free upper ends of the placentas contribute to the occlusion of the locules (Dehn 1992).

In this paper we are dealing only with the first type. Closing bodies are normally easily visible with the naked eye, particularly the larger ones, which can be up to 2 mm in diameter. In an open capsule they are very conspicuous as they are mostly pale and often have a shiny surface, thus contrasting with the dark brown remainder of the capsule. Owing to their prominent appearance, these bodies were already discovered in the early days of botanical exploration of the arid regions of southern Africa. The generic name of the genus *Disphyma* N.E.Br. is derived from the closing bodies (two-lobed in this case).

Much has been said about the function, structure and development of the closing bodies of the Ruschioideae (Berger 1908; Huber 1924; Lockyer 1932; Schwantes 1952, 1957; Volk 1960; Ihlenfeldt 1960, 1971; Haas 1976; Hartmann 1988, 1991, 1993; Hartmann & Gölling 1993; Kurzweil 2005). Comments on the closing bodies of individual species are also found in numerous floristic and taxonomic publications, but most of these are merely descriptions of their shape, size and colour. Detailed investigations and comparisons of these prominent capsule features are rare in literature (Poppendieck 1976; Hartmann 1988), and a number of problems exist, calling for further studies. While the overall appearance of the closing bodies was often used as a diagnostic feature of certain genera and species, there is as yet no clear and well-documented comparative survey of these bodies. Furthermore, information on fruit characters in general is scattered throughout the taxonomic literature and is often not easily accessible (language barrier, some journals not easily obtainable). The present paper aims to review the existing literature on the closing bodies of Mesembryanthema and is supplemented by personal observation. It is hoped that this review will provide the starting point for future research aimed at resolving critical issues regarding the structure and taxonomic implications of the closing bodies of the Ruschioideae.

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MS. received: 2007-04-20.

† The subfamilies Mesembryanthemoideae and Ruschioideae together are termed Mesembryanthema (Hartmann 1991) and represent a group without taxonomic rank.

THE CLOSING BODIES AND THEIR STRUCTURE

Closing bodies are mostly round and often hemispherical protrusions positioned on the fruit wall below the distal ends of the covering membranes at the upper end of the placentas (Figure 1A). Their size ranges from less than 1 mm to 2 mm in diameter. The closing bodies are

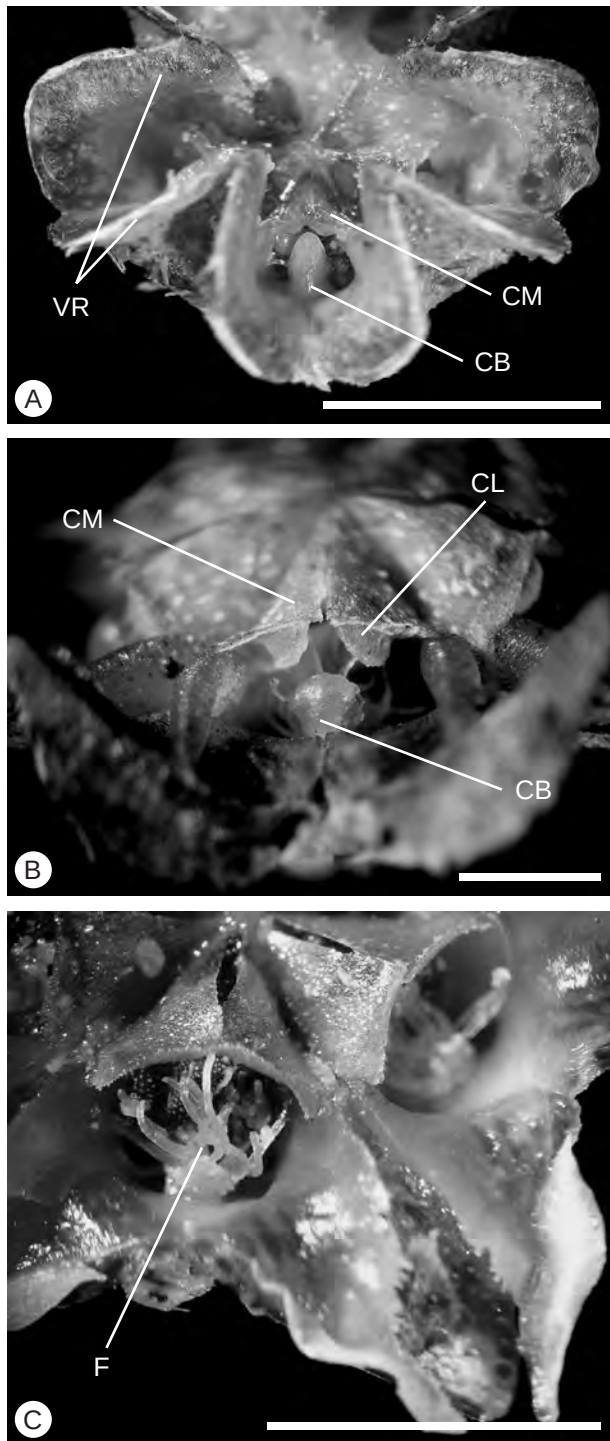


FIGURE 1.—A, *Ruschia lineolata*, Burgoyne 9848: closing bodies formed on fruit wall near upper end of placentas; B, *Ruschia* sp., Burgoyne 8102: closing ledges formed on lower surface of distal end of covering membranes; C, *Lampranthus watermeyeri*, Burgoyne 7562 or *Smicrostigma viride*, Steyn 384: dense bundles of funicles close locules. CB, closing bodies; CL, closing ledges; CM, covering membranes; F, funicles; VR, valve rims. Scale bars: A, 4 mm or 3 mm; B, C, 5 mm.

firmly united with the placentas, the upper ends of the latter often running in a pronounced groove. The larger closing bodies often touch the covering membranes and thus close the locule completely, and in many cases also reach partly under the latter. Small or tiny closing bodies are sometimes rather deeply positioned inside the locule (for example in some genera of the *Eberlanzia* Group). Prominent closing bodies have only been reported in subfamily Ruschioideae, and then only in genera that have complete or nearly complete covering membranes in their capsular fruit (although closing bodies do not occur in all of the genera with covering membranes).

The term 'closing bodies' was originally coined by Steinbrinck (1883). Later Huber (1924) considered these structures as formations of the placentas and consequently termed them 'Plazentarhöcker' (= placental tubercles). This term was subsequently adopted by many textbooks and taxonomic treatments. Ihlenfeldt (1960) on the other hand, interpreted these formations as a product of the endocarp and suggested reverting to the original term 'closing bodies'. After a detailed examination of the closing bodies of *Pleiospilos* N.E.Br., Hartmann & Liede (1986: 458) also rejected Huber's controversial term 'tubercle' as completely inadequate.

The shape of the closing bodies of the Ruschioideae is very diverse. Particularly elaborate closing bodies are found in Hartmann's (1993) *Leipoldtia* Group. They are normally rather large and consist of a 'head' borne on a distinct stalk. Anatomically, the central part is made up of large, spongy cells covered by several cell layers of sclerenchymatic tissue. Smaller rodlet-shaped closing bodies are found in the *Ruschia* type of fruit (Hartmann 1988) and have a similar anatomy. Comparatively small, hook-shaped closing bodies are found in the *Titanopsis* type of fruit, and they consist of sclerenchymatic cells only (Hartmann 1988: 327). The closing bodies of the *Mitrophyllum* type of fruit are not prominent hemispherical bodies, but appear as broad ridges or bosses where the placentas and expanding keels meet (Poppendieck 1976; Ihlenfeldt & Struck 1987). Their epidermis is only moderately thick-walled and an extensive spongy tissue is present. In some genera referred to this fruit type, broad, spongy closing bodies have the shape of ledges and have also been termed as such (Hartmann 1991); the closing ledge of *Dorotheanthus* Schwantes has been referred to as 'Verschlusswall' (= closing sill) (Ihlenfeldt & Struck 1987). Hartmann (1988) suggested that these aforementioned types of closing bodies are not all homologous.

According to their ontogenetic derivation, most of the closing bodies of the Ruschioideae are endocarpal structures. A few other species possess small placental closing bodies, which have a different texture and anatomy (Hartmann 1988). This emerged originally from a careful study of the closing bodies of *Pleiospilos* (Hartmann & Liede 1986) where the following were observed: 1, endocarpal closing bodies are often large, although small and insignificant endocarpal bodies have also been reported occasionally, e.g. *Tanquana* H.E.K. Hartmann & Liede (1986). Endocarpal closing bodies comprise an epidermis of sclerenchymatic cells over a body of isodiametric cells with equally thick walls, the central part of the closing body comprising

either parenchymatic or sclerenchymatic cells. Thus they differ markedly from the cells of the placentas which have unthickened walls throughout. The derivation of these prominent closing bodies from endocarpal tissue has also been found by Kurzweil (2005); 2, placental closing bodies are rare in the Mesembryanthema and contribute only a little to the occlusion of the locule. Examples include *Malephora* N.E.Br., *Pleiospilos nelii* Schwantes, *P. simulans* (Marloth) N.E.Br. and *P. bolusii* (Hook.f.) N.E.Br. (Hartmann & Liede 1986). They are made up of cells with only weakly thickened or unthickened walls, although the cell walls of the epidermis can be strongly thickened. In *Drosanthemum* Schwantes, the endocarp may form a little protrusion, lifting the closing body slightly (Hartmann & Bruckmann 2000: 81).

The genera *Disphyma* and *Rhombophyllum* (Schwantes) Schwantes have two-lobed closing bodies. The situation in a few other genera is somewhat reminiscent of this condition as the closing bodies and their stalks have a more or less deep groove (although this is often largely obscured by the placentas). It is suggested that this partial or complete two-lobed condition is a reflection of the origin from two carpel margins (Kurzweil 2005).

While in most genera the closing bodies are constant in their size and can therefore be used as diagnostic characters, some intraspecific variation was found in *Mitrophyllum* Schwantes (Poppendieck 1976), *Dorotheanthus* subgen. *Dorotheanthus* (Ihlenfeldt & Struck 1987) and *Disphyma* (Chinnock 1996). The shape of the closing bodies of *Odontophorus marlothii* N.E.Br. varies even within the same capsule (Hartmann 1976).

DISTRIBUTION OF CLOSING BODIES IN THE RUSCHIOIDEAE

Only the subgroups of subfamily Ruschioideae are treated here, as closing bodies do not occur in subfamily Mesembryanthemoideae (Figure 2A). The following is a brief review of detailed investigations of the closing bodies of individual genera in the literature. Comparative descriptions and discussions of these structures can also be found in Hartmann (1983, 1988) and Dehn (1992). Overall descriptions of shape, size, colour and consistency of closing bodies are found throughout taxonomic and floristic literature and are not listed here.

The arrangement of the subfamilies and tribes follows the classification of Klak *et al.* (2003). The large subfamily Ruschioideae is divided in four groups (clades), two of these representing the tribes Apatesieae and Dorotheanthae (corresponding to the *Apatesia* and *Claretum* Groups of Hartmann 1993). They form a monophyletic, well-supported group, supported by molecular data (Klak *et al.* 2003). The remaining two clades fall within the tribe Ruschieae in which few DNA sequence changes have been observed (Klak *et al.* 2003). Hartmann (1988) has proposed 10 groups for the species in the tribe Ruschieae. Table 1 gives a short summary of the number of species per taxon, distribution and presence or absence of covering membranes and closing bodies within the Mesembryanthema.

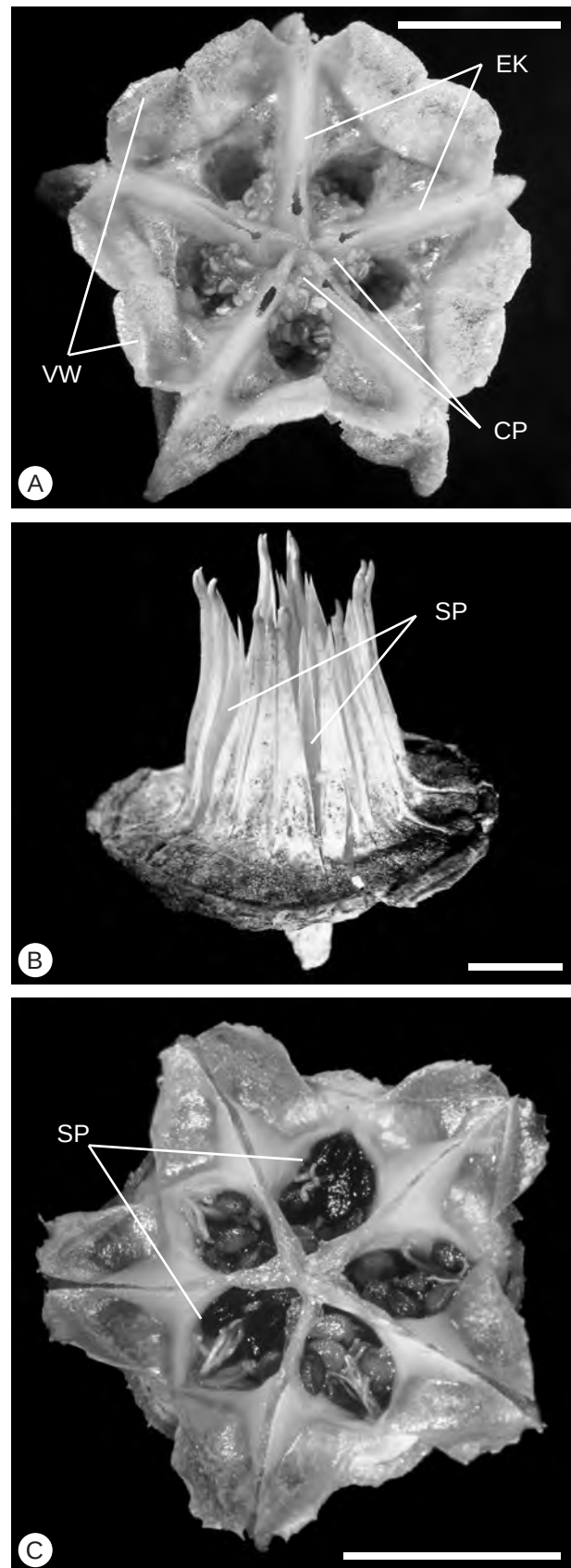


FIGURE 2.—Fruit types. Mesembryanthemoideae: A, *Mesembryanthemum hypertrophicum*, Burgoyne 10349. Tribe Apatesieae: B, *Conicosia pugioniformis* (L.) N.E.Br. subsp. *alborosea* (L.Bolus) Ihlenf. & Gerbault, Burgoyne 10378. Tribe Dorotheanthae: C, *Claretum papulosum* (L.f.) L.Bolus subsp. *papulosum*, Burgoyne 9396(b), showing prominent seed pockets. CP, central placentation; EK, expanding keels (parallel); SP, seed pockets; VW, valve wings. Scale bars: A, 6 mm; B, 10 mm; C, 4 mm.

Tribe **Apatesieae** Ihlenf., Schwantes & Straka

This tribe corresponds to the *Apatesia* Group of Hartmann (1993). Fruit capsules are characterized by the reduction of hygrochasy, absence of valve wings and frequent seed retention in seed pockets (Figure 2B, *Apatesia* type of fruit; Hartmann 1988). The capsules are sometimes schizocarps that break up into mericarps (especially prominent in the genus *Caryotophora* Leistner), which are then dispersed as a whole. Covering membranes as well as closing bodies are absent.

Tribe **Dorotheanthae** (Schwantes ex Ihlenf. & Struck) Chess., Gideon F.Sm. & A.E.van Wyk

The species of this group (corresponding to the *Clereutum* Group of Hartmann 1993) have capsules with or without covering membranes and prominent expanding sheets (Figure 2C). Sometimes they have comparatively insignificant closing bodies (Hartmann 1988, 1991), developed as swellings, spongy sills or ridges but not as large, hemispherical structures as in other Mesembryanthema genera. These closing bodies have a broad base, which is typical of the *Mitrophyllum* type of fruit to which the Dorotheanthae are referred (Hartmann 1988). Ihlenfeldt (1960) and Ihlenfeldt & Struck (1987) also described these ridge-like closing bodies (referred to as 'Verschlusswall' = closing sill), which are found in some species of the genus *Dorotheanthus*. They are best developed in *D. bellidiformis* (Burman) N.E.Br. subsp. *bellidiformis*. Generally, the ridge-like closing bodies of this group are interpreted as a product of the endocarp and not the placenta (Ihlenfeldt 1960: 49). In the genus *Dorotheanthus*, the occurrence of the seven different capsule

types defined on the basis of features of the covering membranes and closing bodies is geographically correlated, and species with capsules that have pronounced closing bodies are more frequent in the southern parts of the distribution area (Ihlenfeldt & Struck 1987).

Tribe **Ruschiae** Ihlenf., Schwantes & Straka

This group comprises most of the Ruschioideae, currently including nearly 1 600 species. An enormous diversity in the capsular fruit structure is found in this group.

Mitrophyllum Group

The capsules have mostly been referred to the *Mitrophyllum* type of fruit (Figure 3A; Hartmann 1988). Covering membranes are mostly complete but are sometimes reduced, and the surface of expanding keels are extended to form flat expanding sheets. Closing bodies are sometimes present, and are mostly developed as spongy sills or ridges and have a broad base. They are rather variable in the extent of their formation but are rarely very large (*Glottiphyllum* (Haw.) N.E.Br.). Valve wings are mostly broad, though sometimes very narrow or absent.

In *Disphyma* the closing bodies are deeply two-lobed (Chinnock 1996). However, in *D. papillatum* Chinnock the closing bodies are variable in size and range from well developed to vestigial, and *D. australe* (Aiton) J.M.Black lacks closing bodies altogether. An abnormal population of this species with variously shaped finger-like outgrowths at the entrance of the locules was reported by Chinnock (1996). *Glottiphyllum* has large

TABLE 1.—Distribution of closing bodies in the Mesembryanthemaceae. Subfamilies and tribes after Klak *et al.* (2003), informal groups after Hartmann (1991, 1993, 1998a). Approximate numbers of species follow Hartmann (1993) and Klak *et al.* (2003, 2007)

Taxon	No. species	Distribution	Covering membranes	Closing bodies
Subfamily Mesembryanthemoideae	± 102	Widespread in South Africa and Namibia; <i>Mesembryanthemum</i> also in coastal areas worldwide	Absent	Absent
Subfamily Ruschioideae				
Tribe Apatesieae	11	Mainly western parts of South Africa, with <i>Conicosia</i> ranging into southern Namibia	Absent	Absent
Tribe Dorotheanthae	11	Western parts of South Africa	Present or absent	Present as a ledge or absent
Tribe Ruschiae				
<i>Mitrophyllum</i> Group	51	Widespread in South Africa, with <i>Disphyma</i> ranging into Australia and New Zealand	Present or absent	Present (broad-based) or absent
<i>Delosperma</i> Group	325	Widespread in southern Africa, with <i>Delosperma</i> ranging into eastern Africa and Yemen	Present or absent	Very rarely present
<i>Stomatium</i> Group	102	South Africa and southern Namibia	Present or absent	Mostly absent
<i>Titanopsis</i> Group	79	Widespread in South Africa and Namibia	Present or absent	Very rarely present
<i>Dracophilus</i> Group	122	Widespread in South Africa and southern Namibia	Mostly reduced	Absent
<i>Bergeranthus</i> Group	54	Widespread in South Africa and southern half of Namibia	Mostly complete	Mostly present, but often small
<i>Lampranthus</i> Group	248	Widespread in South Africa and southern Namibia, with <i>Carpobrotus</i> extending to coastal areas worldwide	Complete	Almost always absent
<i>Ruschia</i> Group	375	Widespread in South Africa and Namibia	Complete, often convex	Small to medium-sized, often hook-shaped
<i>Leipoldtia</i> Group	163	Widespread in South Africa and southern Namibia	Complete, often concave	Large and stalked, rarely small
<i>Eberlanzia</i> Group	17	Western parts of South Africa, southwestern Namibia	Complete	Large or small, sometimes deep in locule

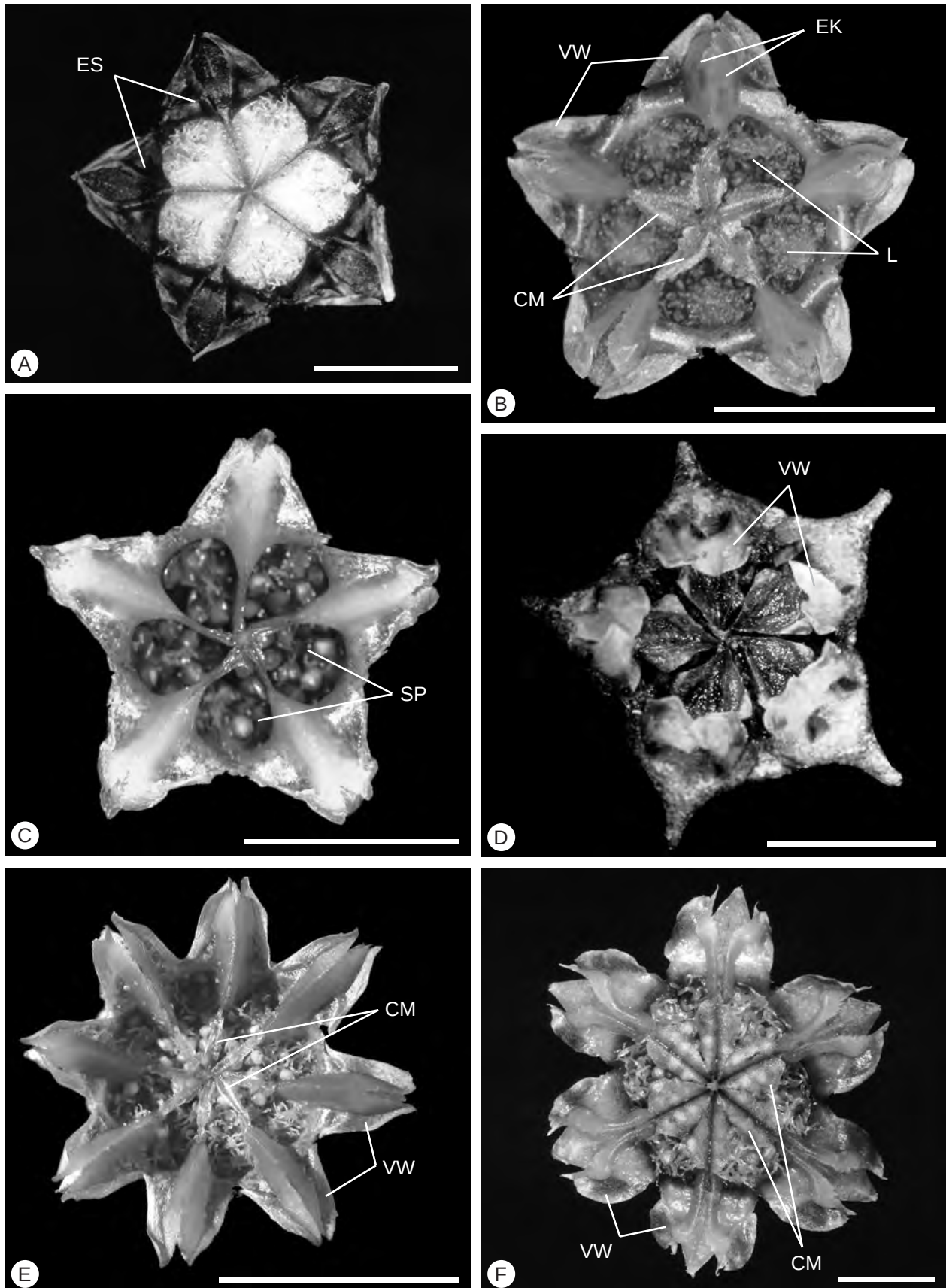


FIGURE 3.—Fruit types. *Mitrophyllum* type: A, *Monilaria chrysoleuca*, Burgoyne 9454B. *Delosperma* type: B, *Delosperma floribundum*, Muller 1776. *Stomatium* type: C, *Stomatium* sp., Burgoyne 8966. *Faucaria* type: D, *Faucaria* sp., Van Jaarsveld 11104, with prominent valve wings borne erect. *Dracophilus* type: E, *Juttadinteria deserticola* (Marloth) Schwantes, Burgoyne 8453B. *Titanopsis* type: F, *Titanopsis calcarea* (Marloth) Schwantes, Burgoyne 9619. CM, covering membranes (reduced); ES, expanding sheets; EK, expanding keels; L, locules; SP, seed pockets; VW, valve wings. Scale bars: A, B, 6 mm; C, 5 mm; D, 4 mm; E, 9 mm; F, 3 mm.

spongy closing bodies with a broad base; their endocarpal origin has been shown by Hartmann & Liede (1986). Hartmann's (1991) concept to include *Glottiphyllum* in the *Mitrophyllum* Group is also supported by features of the expanding tissue (Hartmann & Gölling 1993). Earlier, an alternative concept was proposed by Schwantes (1952) listing this genus under his *Glottiphyllum* type of fruit, together with the genera *Cheiridopsis* N.E.Br., *Pleiospilos* and *Argyroderma* N.E.Br. In *G. difforme* (L.) N.E.Br., *G. fergusoniae* L.Bolus, *G. nelii* N.E.Br. and *G. oligocarpum* L.Bolus, the closing bodies are over-arched by a tongue- or triangle-like tissue of the outer locule wall (Hartmann & Gölling 1993). The closing bodies of various species in the genus *Mitrophyllum* are variable in the extent of their formation even within the same population (Poppendieck 1976). They are generally apparent as swellings or swollen ridges in a position where the placentas and the expanding sheets meet. Anatomically, they are made up of isodiametric cells with strongly thickened walls. The epidermis in their proximal part consists of similar cells but the cells in the distal part are elongate (when seen in a longitudinal section) and have weakly thickened walls, thus resembling the cells of the adjacent expanding tissue.

Delosperma Group

The capsules of this group (Figure 3B) are rather diverse, and the different genera were referred to the *Delosperma* N.E.Br., *Drosanthemum* and *Lampranthus* N.E.Br. types of fruit (Hartmann 1988). Seed pockets occur occasionally. Expanding keels are usually distinct from the expanding sheets and the valves have mostly broad wings. Covering membranes are present or absent. Closing bodies are almost always absent, but the genus *Malephora* often has knobs on the distal end of the placentas which act as closing bodies (Hartmann 1988: 56); these placental closing bodies may also be bilobed. Small and often bilobed endocarpal closing bodies are found in some species of the genus *Drosanthemum*, and most species of this genus have placental closing bodies (Hartmann & Bruckmann 2000).

Stomatium Group

The capsules can mostly be referred to the *Delosperma* and *Drosanthemum* types of fruit of Hartmann (1988). Covering membranes are present or absent, and valve wings are broad to reduced or absent. Seed pockets derived from basal false septa are found in *Stomatium* Schwantes (Figure 3C). Closing bodies are normally absent in the group but small, obscure ones are found in *Orthopterum* L.Bolus.

Herre (1971) stated that distinct bifid closing bodies were also found in *Chasmatophyllum maninum* L.Bolus, whereas they were absent in the rest of this genus. We examined the notes accompanying the protologue made by Bolus (1927), where she stated that capsules of *C. maninum* were not yet available and a drawing of the portion of a capsule of *C. musculinum* (Haw.) Dinter & Schwantes was given, showing bifid closing bodies. Both Bolus and Herre made an error in citing bifid closing bodies for *Chasmatophyllum maninum*. Examination by the authors of many recently collected specimens of *C. musculinum* has shown no bifid closing bodies.

Hartmann (1988) placed *Faucaria* Schwantes and *Orthopterum* in this group, but for an alternative view, which is followed below, see Groen & Van der Maesen (1999).

Faucaria Group

This group corresponds to the section established by Schwantes (1952) and reinstated by Groen & Van der Maesen (1999) and comprises only two genera (*Faucaria* and *Orthopterum*) as their capsules are unique (Figure 3D). When the capsules are viewed after wetting, one gets the impression that they are empty, as locules are hidden by lamellae curving over the top of the locules. The capsules are 5(6)-locular and are deep, the valves with fissures between them. Conventional covering membranes and closing bodies are absent and expanding keels end in an awn. The deep locules combined with curved lamellae are highly effective in retaining seeds during periods of low rainfall. Capsules can become detached after ripening by being pushed out by the enlarging leaf pair produced the following season and may roll away, but are never found more than a few centimetres from the parent plants (Groen & Van der Maesen 1999). Particularly prominent valve wings are found in *Faucaria* where they are borne erect when the capsule is open. When dry, these valve wings fold back into thin grooves. *Orthopterum* has similar fruits with their septa separated into two parts, the upper part arching on top of the capsule.

Titanopsis Group

The capsules of this group (Figure 3F), mostly referred to Hartmann's (1988) *Titanopsis* Schwantes and *Delosperma* types, have well-developed or reduced covering membranes and broad valve wings which taper distally. Closing bodies are mostly absent, although they are developed as tiny (rarely prominent) structures in some species of *Aloinopsis* Schwantes, *Tanquana* and *Ihlenfeldtia* H.E.K.Hartmann.

The genus *Ihlenfeldtia* was established to include two species previously included in *Cheiridopsis* (Hartmann 1992). This genus is characterized by its distinct fruit morphology, with mostly 10 locules, thin, straight, complete covering membranes, and valve wings that are broad at the base. Endocarpal closing bodies are present and are illustrated by line drawings in Hartmann's publication. Anatomically, they comprise a translucent layer of vertical cells on top of a sclerenchymatic body. The small genus *Tanquana* was separated from *Pleiospilos* as it differs in several characters including its fruit structure (Hartmann & Liede 1986). Capsules were shown to be generally less robust than those of *Pleiospilos*, having thinner valves and covering membranes. Important distinguishing features were found in the structure of the closing bodies, which are small and of endocarpal origin.

Dracophilus Group

Fruits of this group (Figure 3E) mostly belong to the *Delosperma* type of capsule (Hartmann 1988). Covering membranes are mostly reduced to form a narrow rim, and valve wings are usually prominent. Closing bodies are generally absent.

Bergeranthus Group

This group has fruits that are close to the *Mitrophylum* type of Hartmann (1988) but generally have stout and firm covering membranes (Figure 4A). The valve wings are mostly reduced to narrow organs and are often awn-like; occasionally they are absent altogether. Closing bodies are present or absent.

The spongy closing bodies of *Bergeranthus* Schwantes are rather large plates (Schwantes 1952: 16; Hartmann 1993: 61). In *Cerochlamys* N.E.Br., the small closing bodies are of placental origin and they are frequently over-arched by a translucent layer of tissue that is derived from the expanding sheets (Hartmann 1998b: 52). The placental closing bodies of *Hereroa* (Schwantes) Dinter & Schwantes are tiny (Hartmann 1993: 61). In this genus the locule entrance is often closed by long funicles (Dehn 1992: 135). Small and frequently deeply set closing bodies are found in *Machairophyllum* Schwantes where they may be irregular in shape (Kurzweil & Chesselet 2003). *Rhombophyllum* species have large, flat or rounded and bipartite closing bodies (Schwantes 1952: 15–17; Hartmann 1993: 61).

Lampranthus Group

Most genera of this group have capsules of the *Lampranthus* type (Figure 4B; Hartmann 1988). While hygrochastic capsules are the norm, *Carpobrotus* N.E.Br. species differ by being the only genus within the tribe Ruschieae to have indehiscent fleshy berries (Figure 5A). Locules have rigid covering membranes with additional closing devices at the distal end. Together with sterile funicles, these closing devices on the underside of the covering membranes are largely responsible for closing the entrance to the locule. Valve wings are present or absent. Prominent closing bodies have only been reported in the genus *Enarganthe* N.E.Br. (Herre 1971) but are absent in all other genera.

Ruschia Group

This is a large group with fruits mostly of the *Ruschia* type (Figure 4C; Hartmann 1988). Fruits normally remain on the plants (occasionally up to several years) and release the seeds after dehiscence, but tumble fruits are found in *Khadia* N.E.Br. and rarely also in *Ruschia* Schwantes. The frequently deep locules have firm, complete covering membranes with additional closing devices at the distal end. Expanding keels are often widely diverging and valve wings are mostly absent or reduced. Closing bodies are small or medium-sized and hook- or rodlet-shaped. They are comparatively large in *Acrodon* N.E.Br. (Burgoyne 1998), a genus with a capsule structure that is somewhat reminiscent of the *Leipoldtia* type of fruit according to Hartmann (1988).

An endocarpal closing body that is largely covered by the placenta was reported in *Ebracteola montis-moltkei* (Dinter) Dinter & Schwantes (Hartmann 1996: 39). Closing bodies of *Khadia* are of complex composition (Chesselet & Hartmann 1995; Chesselet *et al.* 1998), and the various types can be used to identify the different species of the genus: the 'closing bodies' are either prominent placental formations or endocarpal protrusions and

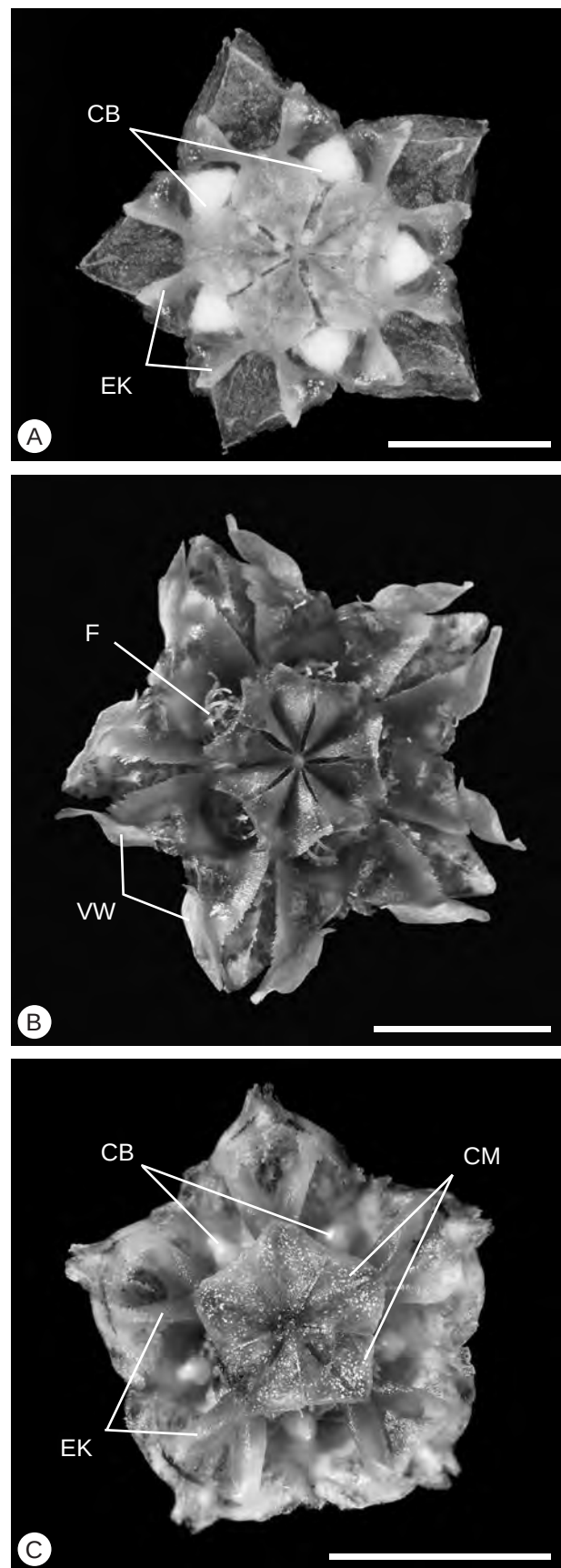


FIGURE 4.—Fruit types. *Bergeranthus* type: A, *Bergeranthus multi-ceps* (Salm-Dyck) Schwantes, Burgoyne 8918. *Lampranthus* type: B, *Lampranthus watermeyer*, Burgoyne 7562. *Ruschia* type: C, *Ruschia maxima* (Haw.) L.Bolus, Burgoyne 8767. CB, closing bodies; CM, covering membranes; EK, expanding keels; F, funicles; VW, valve wings. Scale bars: A, 4 mm; B, 7 mm; C, 5 mm.

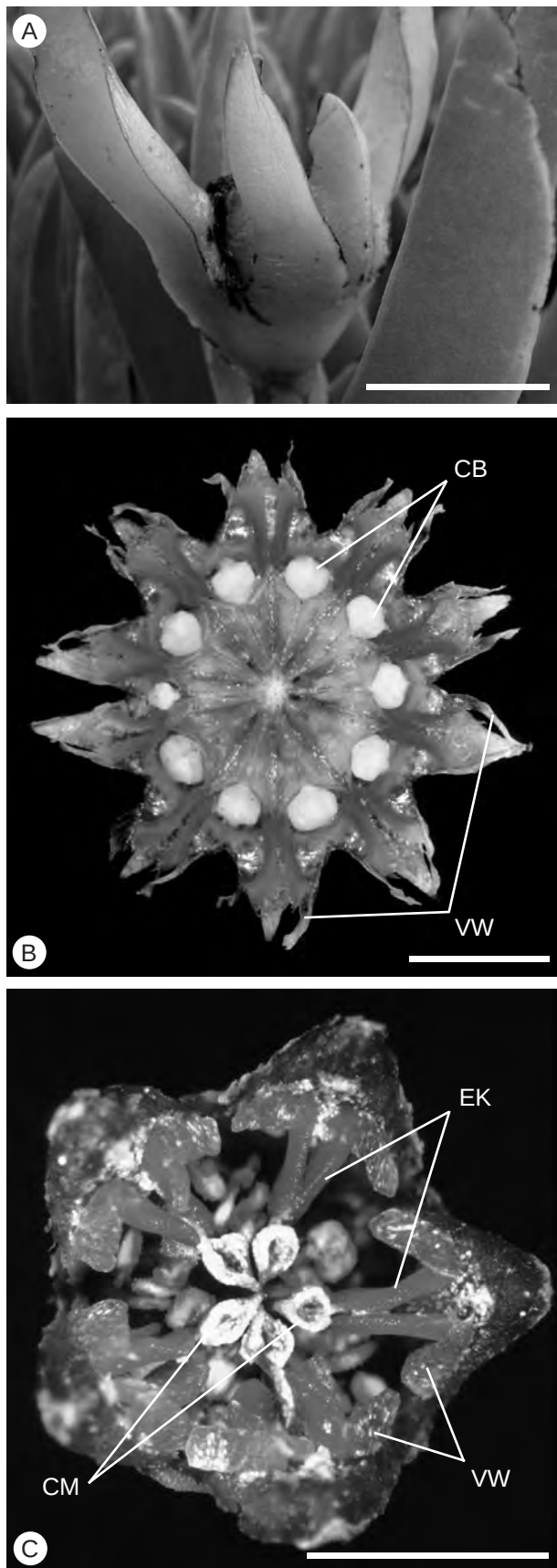


FIGURE 5.—Fruit types. Fleshy in A, *Carpobrotus edulis* (L.) L.Bolus subsp. *edulis*, Burgoyne 6317. *Leipoldtia* type: B, *Cheiridopsis namaquensis* (Sond.) H.E.K.Hartmann, Burgoyne 9487. *Eberlanzia* type: C, *Stoeberia frutescens* (L.Bolus) Van Jaarsv., Burgoyne 10323. CB, closing bodies; CM, covering membranes; EK, expanding keels; VW, valve wings. Scale bars: A, 25 mm; B, 5 mm; C, 4 mm.

are partly covered by some outgrowth of the expanding sheets. Dehn (1992) showed that the endocarpal closing bodies of *Ruschia* are comprised mainly of irregular, thin-walled cells, and are covered by 3–6 layers of prosenchymatic and moderately thick-walled cells plus a one-layered sclerenchymatic epidermis, which corresponds well with the observations of Hartmann & Liede (1986). Based on structure, six types of closing bodies were distinguished by Hartmann & Liede (1986) in the study of *Ruschia* and related genera.

Leipoldtia Group

Most genera of this group were referred to the *Leipoldtia* type of fruit (Figure 5B; Hartmann 1988), characterized by: 1, persistent, $\pm$ concave, complete covering membranes that frequently have additional closing devices in the form of bosses or ledges; 2, mostly large and distinctly stalked closing bodies; 3, broad (rarely reduced) valve wings.

Capsules normally remain on the plant but tumble fruits are known in *Fenestraria* N.E.Br. and *Cephalophyllum* N.E.Br. This is the only group of Mesembryanthema in which the closing bodies are consistently present as prominent structures. They are also large in most genera—comparatively small closing bodies are found only in *Fenestraria* (Hartmann 1982), *Jordaaniella* H.E.K. Hartmann (Hartmann 1984) and *Cylindrophyllum* Schwantes (Herre 1971). Their surface is often rugose (Hartmann 1991: 124). The texture of the closing bodies of this group is corky, with sclerenchymatic outer layers. Most genera of this group have been taxonomically revised by H.E.K. Hartmann (several papers, see below; sometimes with co-workers), with detailed comments on many plant features including the closing bodies.

As part of a detailed study of the genus *Antimima* N.E.Br. emend Dehn, Dehn (1988) described the closing bodies and illustrated them by means of line drawings and SEM micrographs. The large closing bodies are short-stalked and of endocarpal origin. Hartmann (1977) revised the genus *Argyroderma* and examined the late development of the closing bodies of *A. congregatum* L.Bolus. It was shown that the cells of the closing bodies still have unthickened walls at the time of anthesis and become thickened only later. The structure and position of the closing bodies of the genus *Cephalophyllum* was described by Hartmann (1978). According to Hartmann & Dehn (1987), species of *Cheiridopsis* have large closing bodies in the mature fruits, which often partly reach under the distal parts of the covering membranes and close their entrance entirely. No taxonomic correlation of the different types of closing bodies was found. An informative SEM micrograph of the stalked closing body of *Leipoldtia schultzei* (Schlechter & Diels) Friedrich was shown by Hartmann & Rust (1994). The shape and surface of the closing bodies of *Odontophorus marlothii* was found to be variable within one population and even within the same capsule, and can therefore not be used as a diagnostic feature (Hartmann 1976). The genus *Pleiospilos* was examined in detail by Hartmann & Liede (1986). It was shown that the five species of *P.* subgenus *Punctillaria* have large endocarpal closing bodies that close the locule entrance almost completely and are entirely made up of sclerenchymatic cells. The epidermis cells are elongate (vertically arranged), whereas the cells of subja-

cent layers are isodiametric. The three species of *P.* subgenus *Pleiospilos* have small placental closing bodies comprising isodiametric cells with unthickened walls although their epidermis cells can have slightly thickened walls.

In our opinion, *Antimima* and *Cylindrophyllum* do not belong in the *Leipoldtia* Group. *Antimima* is better placed within the *Ruschia* Group and *Cylindrophyllum* belongs in the *Bergeranthus* Group.

Eberlanzia Group

This small informal group was established by Hartmann (1998a). In *Eberlanzia* Schwantes (Figure 5C) and *Amphibolia* L.Bolus, the fruit structure is similar to that of *Ruschia* except for the broad valve wings. Closing bodies in the group are small or large, sometimes deeply set in the locule. Fruits breaking up into nutlets are found in *Stoeberia* Dinter & Schwantes where the anemochoric seeds are also unusual. SEM illustrations of closing bodies of *Amphibolia laevis* (Aiton) H.E.K.Hartmann were shown by Hartmann & Dehn (1989).

FUNCTIONAL ASPECTS

Seed dispersal in the Mesembryanthemaceae is defined as ombrohydrochorous, i.e. triggered by rain drops. The covering membranes, which prevent the simple washing-out of the seeds, always comprise two parts that are arranged roof-like but are never fused on top. It has been shown that the association of flexible covering membranes and prominent closing bodies results in an increased water pressure in the locule after a direct hit by a rain drop (Parolin 2006), and consequently the seeds are expelled jet-like, following a bending of the covering membranes (Berger 1908; Lockyer 1932; Schwantes 1952). Lockyer (1932) showed that this complete occlusion of the locule actually promoted dissemination in space, as jet-like expelled seeds fell further from the parent plant than merely washed-out seeds would. The same mechanism also protracts dispersal in time, i.e. results in slow or delayed release of the seeds (Ihlenfeldt 1971), and this is obviously ecologically advantageous in the arid habitat of the Mesembryanthemaceae. The role of the small closing bodies of some species that close the distal entrance of the covering membranes only partly is not fully understood as yet, e.g. *Tanquana* (Hartmann 1983: 37; Hartmann & Liede 1986: 461). Those species that lack prominent closing bodies altogether often have other devices to achieve the occlusion of the locules, such as protrusions from the covering membranes in the form of ledges, sills, bulges or rodlets, by sterile funicles or by free ends of placentas. This seems to suggest that the occlusion of the locules is favoured by natural selection but is achieved by different means. Capsule types that have only very incomplete or no covering membranes are clearly less efficient with regard to their seed dispersal (e.g. Ihlenfeldt & Struck 1987). These species also tend to be found in areas of higher rainfall (e.g. *Delosperma*), where it is not critical if seed is disseminated in one rainfall event if this is closely followed by more rain.

From an evolutionary point of view, certain adaptive pressures on dispersal mechanisms can influence the

size and shape of the closing bodies, as they are obviously correlated with the dispersal syndrome. This was illustrated by Hartmann (1988: 329) in the example of *Fenestraria*—this species is dispersed as tumble fruits, and therefore only small closing bodies have evolved in its capsules.

TAXONOMIC SIGNIFICANCE

In view of our incomplete knowledge of the closing bodies of the Mesembryanthemaceae, it is premature to make firm proposals regarding the taxonomic significance of their structure. Owing to the variation observed in some genera and the only sporadic occurrence of these bodies, it is unlikely that extensive studies will eventually yield taxonomically significant features. While the structure of the closing bodies does not permit a new classification, some correlations to fruit types can be observed (Hartmann 1988: 327). Nevertheless, the structure and size of the closing bodies can mostly be used as diagnostic features of individual species and genera, and partly also of larger informal groups (Hartmann 1991, 1993).

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OBITUARY

ROBERT BAILY DRUMMOND (1924–2008)

Many people from all walks of life interested in something to do with plants visited the National Herbarium, now in the Botanic Gardens in Harare, and came across Bob Drummond, and probably most people who met him won't forget the experience. Bob was very much his own person. Usually, he was interested and charming, but he could also be non-committal, abrupt or even downright rude. He was as interested in people as he was in plants and his memory of the people he had met was as remarkable as his knowledge of the plants. When identifying a plant, which he seemed to be able to do almost regardless of the state of the specimen, he would want to know about both the plant and the person and where they both came from, which he also remembered. In fact Bob Drummond was an institution at the herbarium for 38 years, much of the time as Curator, and even after he had retired he was often there. His knowledge of all aspects of the flora was phenomenal, and his passing away leaves a gap in botanical knowledge that will probably never be filled.

Robert (Bob) Baily Drummond (Figure 1) was born in Petersfield, Hampshire in the UK on 27 February 1924, and died at his home in Harare on 3 June 2008 aged 84. He grew up in Leeds where his father worked in the Department of Agriculture at the local university. As a child, Bob collected plants and became familiar with the British flora. An interest probably fostered by his mother, a keen member of the British Wild Flower Society, to which she submitted her flowering plant records each year. When he was 14, he travelled with an aunt to the United States for four months to see relatives, visiting New Orleans, the Grand Canyon, Yosemite and the West Coast, a trip that probably broadened his knowledge of plant diversity.

Bob attended Leeds Grammar School from 1932 to 1942, studying classics and obtaining A-level passes in both Latin and Greek and then continued to study them for the next year at Leeds University. He was very proud of his knowledge of those subjects and regarded his training in them as the perfect preparation for a botanist. In 1943 he volunteered for the Royal Navy, serving as a coder in Sydney, Australia with the British Pacific Fleet. In 1946 he was released from the Navy, returning to Leeds University, where he then studied Botany and Zoology, obtaining a B.Sc. in 1948 at which stage he was reputed to have been able to identify and name every plant in the United Kingdom.

He started his professional career as a botanist in January 1949 when he was appointed by the Colonial Office as an Experimental Officer at the Kew Herbarium working on the *Flora of tropical East Africa*. It was here that Bob acquired a sound knowledge of the African flora through his interest in sorting specimens into families and genera. Bob's first major collecting trip was the first Colonial Office Expedition to East Africa with J.H. (Jim)

Hemsley in 1953. The primary aim was to visit some of the localities collected by German botanists earlier in the century, many of their specimens having been destroyed during the bombing of Berlin. They left in January 1953 for nine months, collecting in northeastern Tanzania (especially the Usambara, Nguru and Uluguru Mountains), in coastal Kenya and Uganda west of Lake Victoria. Their outstanding collection of around 4 800 numbers is said to be one of the most comprehensive from East Africa (Polhill, Polhill & Robertson in prep.), and duplicates were sent to, amongst others, the Nairobi, Lisbon, Missouri and Pretoria herbaria. Bob once commented that in those days, before plastic bags, specimens had to be put straight into the press which was very time consuming in the field.

It was at Kew that he met his future wife, Joan Morris, at that time a technician working for Noel Sandwith on tropical American plants. They married in 1955 just before Bob took up a botanical post in the then Southern Rhodesia Government Herbarium (SRGH) in Salisbury (now Harare, Zimbabwe) in May 1955. In those days the herbarium was housed in a corrugated iron shed at the Research and Specialist Services complex. The post was created largely to enable Hiram Wild, the then Government Botanist to spend a lengthy period at Kew to make a start writing volume 1 of the recently begun *Flora zambesiaca* in collaboration with Arthur Exell. It was in



FIGURE 1.—Robert (Bob) Baily Drummond (1924–2008).

Harare that Bob and Joan spent the rest of their married lives and where their two daughters, Jean and Janet were born.

Bob undertook a number of major collecting trips: to the Makgadikgadi Pans in northern Botswana in April 1957 with Stanley Seagrief, to western Zambia in November 1959 with J. Cookson, to Zambia's North-western Province in March 1961 with R.O.B. Rutherford-Smith, and to Mwinilunga in the same area with Graham Williamson in June 1963.

Graham Williamson recalls that 'during our trips we would collect large numbers of plants placing them in sealed plastic bags. At our campsites at night I would set up a table and start up a Honda generator lighting two bulbs, one clear, linked to the table so Bob could sort and press the plants, the other, an ultra-violet light some distance from our camp so I could collect, throughout the night, moths and other insects'; and he goes on, 'Many of the expeditions were extremely hazardous especially during the rains. One such occasion we almost lost the 4 × 4 vehicle which was perched precariously on a pont while crossing the swollen Kalungushi River. Often Bob would wet the pressings with petrol—while smoking. During camp stops of more than a day we would lie our wet papers in long lines to sun dry'.

Bob Drummond visited Botswana in 1965 with Hiram Wild and again with Helen Moss, Richard Mithen and Helen Kibblewhite in the mid 1980s. In addition, Bob made extensive collections from various parts of Zimbabwe, particularly the mountainous eastern parts and dry southern lowveld between the late 1950s to early 1970s; two that he mentioned were to the Chimanmani with John Ngoni, Steven Mavi and Rosemary Grosvenor during which all collections were recorded as Grosvenor numbers, and in 1971 to Gonarezhou with John Ngoni and Steven Mavi. His collecting numbers totalled over 10 000.

In his enthusiasm, Bob Drummond was always so willing to share his knowledge and he played a major part in early schoolboy expeditions. Even when he did not accompany expeditions he briefed them before the trip, showing the boys how to collect and press plants correctly and advising them on keeping a notebook with their collection records, and then helped them identify their specimens when they returned.

He accompanied the Rhodesia Schools Exploration Society expeditions to Mateke Hills in 1958. John Loveridge, a 16 year-old schoolboy sitting on the back of a lorry waiting to depart, first saw Bob as a tall, fair man with red cheeks who was collecting weeds on the roadside and putting them into a plant press. He found Bob 'the walking encyclopaedia of plant names that I needed! He seemed to know everything, and I just soaked up the names, and vegetation types, some of which I remember clearly to this day'. The report of the Mateke expedition records that 426 species and subspecies of vascular plants were collected in two weeks.

John goes on: 'From those idyllic expedition days I stayed in touch with Bob. I sent him plants collected from around Gwelo and from our family 100-acre plot in

Melsetter, now Chimanmani, and received neat lists of his determinations at regular intervals. I also collected plants on the Rhodesia Schools Exploration Society Midlands Branch expeditions to Sanyati and Sabi-Lundi junction and on the Matabeleland branch's expedition to Sentinel Ranch. Like Bryan Simon, I was stimulated in my botanical interests by Bob's genuinely caring attitude that I should receive names for plants I collected as quickly as possible'.

Other Rhodesia Schools Exploration Society expeditions that Bob went on were to Tuli in 1959 and to Buffalo Bend in 1961. Bryan Simon writes: 'I collected many grasses on the expedition when Bob was leader of the botany group to which I was assigned, and I became impressed what attention had to be given in pressing specimens, especially when it was windy and teamwork was the order of the day'.

I remember when Bob came on a Tree Society trip in 1985 to Ruckometje Camp on the Zambezi River at Mana. This was towards the end of April and there had been late, very heavy rains and the rivers were flooded, so everywhere they went they had to walk, including through the flooded rivers. One walk, having forded the river up to our waists in water, was more or less an all-day affair. We reached a pre-arranged point and travelled back by canoe. But in the meantime it was very hot and we seemed to go on for ever. At one stage Bob appeared to have got left behind and I was getting seriously worried—and then the somewhat overweight Bob reappeared, rather flushed with the heat, a huge fertiliser bag full of plant material in his hand and a very smug look on his face. He had had a wonderful time. Had we seen this and had we seen that and of course we hadn't, but he had.

Bob had an eye for all plants of interest and an uncanny ability to spot small, insignificant ones, and recognize something as being different. For instance his discovery of the monospecific *Triceratella drummondii* (Commelinaceae) in 1957 whilst sitting having lunch. He recognized it as new, and sent it to Brennan at Kew, who soon described it. Bob was the only person to find it again—in the same place 10 years later—until 30 years later when it turned up on sand dunes on the Mozambique coast, some 1 000 km away. Many of his collections became type specimens for newly described species. Furthermore, he had 13 species of plant named after him.

Bob was as interested in people as he was in plants and he would spend hours talking with visitors to the Herbarium. He had the exceptional ability to name anything from small sterile scraps to fertile material, and to recognize what was a new record. Anyone who brought specimens was encouraged to collect more and shown how to do this better, and was helped with identification. Bob was a true botanist in the widest sense, willing to identify the plants in any family. And he was as at home in the field as he was in the herbarium.

In later life, when wanting plants identified, if the person was prepared to work with him he would set about identifying the specimens immediately, clearing bench space, and bringing bundles of named specimens

from the cupboards for comparison. While engaged in this work he was constantly interrupted by other people, either requiring his professional services or casual visitors, interruptions he enjoyed, or by workers in the herbarium or botanic garden wanting to borrow money (but no one was ever seen coming to repay him). Identifying a batch of specimens could take several days, sometimes necessitating returning to the herbarium at weekends, or after supper and working late at night in order to get the job done.

It was this attitude and support, that paid no attention to working hours or days, which encouraged many people to make collections throughout the *Flora zambesiaca* region. When he was the Curator, the National Herbarium was always kept up to date and became the main centre of knowledge of the region, attracting many researchers and other visitors.

Although Bob didn't publish much himself, his contribution to many other authors is acknowledged in numerous books including *Keith Coates Palgrave's Trees of southern Africa* to which he made an enormous and invaluable contribution, including checking the whole of the original text. It was a lot of work and not very stimulating for Bob so Keith had to use a lot of patience to persuade him to keep at it. He used to give Bob about 30 pages at a time and sometimes when he returned the checked pages his comment was 'You can't say that'. Whether Keith did or did not follow his advice I don't remember.

From 1968 to 1994, Bob Drummond was associated with the journal *Kirkia*, now known as the *Zimbabwe Journal of Botany*, in the roles of Co-editor, Assistant Editor and Consultant.

Bob Drummond was made an Honorary Vice President of the Aloe, Cactus and Succulent Society of Zimbabwe in recognition of his contributions to the Society since its establishment in 1969. Michael Kimberly said that when the first issue of *Excelsa*, the illustrated journal of the Aloe, Cactus and Succulent Society of Zimbabwe

was compiled in 1971, Bob assisted and read through the entire text and made all necessary corrections to ensure the botanical accuracy of the contents. He assisted in the same way with 12 of the subsequent volumes of *Excelsa*. Likewise, with the *Excelsa Taxonomic Series*, which contained the revisionary work by L.C. Leach on the Euporbiaceae and the Stapeliaceae, Bob was most helpful and generous with his advice and assistance.

There are many articles, papers and reports where Bob Drummond's help is acknowledged. Many authors owe him a great debt for naming their specimens and pointing out what was known already and what was of particular interest. And probably his greatest contribution was the huge amount of information he so willingly passed on verbally to one and all. He certainly influenced and assisted many people and I was very privileged to be one of those people and to acknowledge it with grateful thanks.

There are 13 species which were named after R.B. Drummond: Acanthaceae: *Blepharis drummondii* Vollesen (2000); Asteraceae/Compositae: *Bidens drummondii* Wild (1967), now included under *Bidens oligoflora* (Klatt) Wild; Asteraceae/Compositae: *Emiliella drummondii* Torre (1975); Celastraceae: *Maytenus drummondii* N.Robson & Sebsebe (1987), now under *Gymnosporia drummondii* (N.Robson & Sebsebe) Jordaan; Commelinaceae: *Triceratella drummondii* Brenan (1961); Leguminosae: Papilionoideae: *Crotalaria drummondii* Milne-Redhead (1961), now under *Crotalaria scassellatii* Chiov.; Leguminosae: Papilionoideae: *Tephrosia lurida* Sond. var. *drummondii* Brummitt (1968); *Tephrosia longipes* var. *drummondii* (Brummitt) Brummitt; Loranthaceae: *Englerina drummondii* Polhill & Wiens (1998); Lythraceae: *Nesaea drummondii* A.Fernandes (1974); Orchidaceae: *Oligophyton drummondii* H.P.Linder & G.Will. (2000), now under *Benthamia drummondii* (H.P.Linder & G.Will.) Szlach. & Rutk.; Podostemaceae: *Leiothylax drummondii* C. Cusset (1980); Rubiaceae: *Tarenna drummondii* Bridson (1979); Rutaceae: *Vepris drummondii* Mendonça (1961).

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Book Review

MOLTENO FERNS: LATE TRIASSIC BIODIVERSITY IN SOUTHERN AFRICA by H.M. ANDERSON & J.M. ANDERSON. *Strelitzia* 21, 2008. *South African National Biodiversity Institute, Pretoria*. Pp. 260. Soft cover: ISBN 978-1-919976-36-5, price R180.00, \$45.00.

Several decades of sustained, almost heroic, efforts by Heidi and John Anderson have established the Late Triassic Molteno fossil flora of southern Africa as one of the most complete windows into the plant life of the past. In palaeobotany, as in other areas of science, the norms and pressures of academia tend to encourage an approach that focuses on individual plant fossils, usually starting with the best preserved and most informative. In many ways this makes sense. After all, we all want to maximize the outcomes from our labours, and setting priorities is routine in all areas of life today. But in palaeobotany, what we risk losing by focusing just on the best fossils and treating them one-by-one, is a broader sense of context. Very often when we read an account of a fascinating new fossil we are left with important but unanswered questions. What was the whole fossil assemblage like? How abundant was this species compared to other species? In what kind of plant communities did this species most likely occur? The landmark studies by Heidi and John Anderson address and provide answers to these questions and more. They provide excellent descriptions and illustrations of important fossil plant species, but they do so in the context of rigorous documentation of whole plant assemblages, and indeed the entire Molteno fossil flora. Their careful attention to detail, combined with painstaking documentation and careful synthesis, provides a more complete picture, and a picture that will stand the test of time.

This fourth volume in the Molteno series focuses on the ferns. It takes a similar approach to the three earlier landmark volumes, which dealt with *Dicroidium* (and a preliminary photographic overview of the entire flora), seed plant foliage, and seed plant reproductive structures. This volume, once again, is a comprehensive treatment and there are the trademark tables with occurrences scored by the 50 different fossil assemblages that include fossil ferns. Altogether there are 37 species assigned to 16 genera and three higher groups. And in this work the Molteno itself is placed in context. There is a very useful and detailed tabulated review of fern floras from elsewhere in Gondwana.

As in previous publications on the Molteno, all of the fern material described is beautifully illustrated with black-and-white photographs, as well as detailed drawings. But an excellent innovation in this time around is the inclusion of 52 beautiful colour plates illustrating the most important specimens. These plates give a much better impression of the quality of the Molteno fossils and the nature of their preservation. They are the next best thing to seeing the fossils themselves.

The Molteno flora provides a fascinating glimpse into the transition between the terrestrial plant communities of the Palaeozoic and those of the Mesozoic. In terms of the ferns, the presence of Marattiaceae provides continuity between the ancient eusporangiate groups of the Palaeozoic and the handful of genera in that group that still persist today. But on the other hand, the presence of unequivocal Dipteraceae heralds the appearance of the leptosporangiate fern groups that diversify through the later Mesozoic and Cenozoic. And most conspicuous in the fossil fern assemblage of the Molteno is foliage of Osmundaceae. *Osmundopsis*, *Rooitodites*, *Birtodites* and *Elantodites* are especially well represented. But there are also half-a-dozen other genera, all of probable osmundaceous affinity, that are known only from sterile material. In recent analyses of fern phylogeny, based on both molecular and morphological data, Osmundaceae are placed securely in an intermediate position between eusporangiate and leptosporangiate groups, as sister to all other leptosporangiate ferns. The composition of the Molteno fern flora makes complete sense in its broader temporal and systematic context.

It is a wonderful testament to the tenacity of Heidi and John Anderson's fieldwork that about half of all the fern species from the Molteno flora are known from fertile specimens. There is exquisite fertile material of *Asterotheca*, but most prominent are fertile specimens of Osmundaceae. In some specimens the thickened walls of the annular cells are exquisitely illustrated in the colour plates. The only disappointment is that none of these specimens is sufficiently well preserved to yield spores. Some of the specimens (for example *Elantodites alisoniae* from Bird River) look promising, but so far, in all cases, it has not been possible to isolate spores or cuticles.

Like the three previous volumes on other plants of the Molteno flora, the treatment of the ferns is a tour de force. Its comprehensive approach to thoroughly documenting a major component of the flora is increasingly uncommon in modern palaeobotany, but it is an approach that is simply invaluable. It should be a reminder to all of us that it is not just important to document the trees but also to step back and see the forest. In this volume, as in the others in this series, Heidi and John Anderson have managed to do both—and in spectacular style.

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