

# Flowering Plants of Africa

Volume 68

June 2023



# Flowering Plants of Africa

Since its inception in 1921, this serial, modelled on the former *Curtis's Botanical Magazine*, has published well over 2 000 colour plates of African plants prepared by some 80 artists.

The object of the journal is to convey to the reader the beauty and variety of form of the African flora, to stimulate an interest in the study, conservation and cultivation of African plants, and to advance the science of botany as well as botanical art.

The illustrations were previously prepared by artists on the staff of the South African National Biodiversity Institute (SANBI). We welcome contributions of suitable artistic and scientific merit. Please see *Guide for authors and artists* on page 219.

## **History of this series**

(note Afrikaans translation and changes in title)

### **Volume 1 (1921) to volume 24 (1944):**

*The Flowering Plants of South Africa*

### **Volume 25 (1945–1946) to volume 26 (1947):**

*The Flowering Plants of Africa*

### **Volume 27 (1948–1949) to volume 52 (1992–1993):**

*The Flowering Plants of Africa*

*Die Blomplante van Afrika*

### **Volume 53 (1994) to volume 68 (2023):**

*Flowering Plants of Africa*

**Cover illustration:** *Tephrosia monticola* (Plate 2391)

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# Flowering Plants of Africa

A peer-reviewed journal containing colour plates with  
descriptions of flowering plants of Africa and  
neighbouring islands

Volume 68



Pretoria  
2023

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*This volume is dedicated to*

**ESTRELA PAULA DAS NEVES FIGUEIREDO, Ph.D. (10 May 1963– )**

During a career of more than 40 years as a plant scientist, Prof. Estrela Figueiredo was tenured at the Instituto de Investigação Científica Tropical, Lisboa, Portugal, after which she assumed associate positions at the South African National Biodiversity Institute and the University of Pretoria. She is at present attached to the Nelson Mandela University in Gqeberha. As plant systematist she has focussed virtually her entire career on the flora of Africa, including contributing taxonomic studies in families such as the Acanthaceae, Rubiaceae, Asphodelaceae and Crassulaceae. As part of this work, Estrela has mentored and trained several students and young scientists.



Prof. Estrela Figueiredo in 2022.

Since 1996 Estrela worked on a wide range of aspects of the flora of Angola. In a global first she jointly produced four essential biodiversity tools for the country in short order: a definitive floristic checklist, a comprehensive catalogue of common names, a catalogue of the exotic flora, and a complete treatise on the botanical exploration of the country. Few countries globally have ready access to such works produced in the modern era.

She has participated in several international biodiversity thrusts, including in the Global Biodiversity Information Facility, the African Plants Initiative and the Global Plants Initiative.

Estrela is a prolific author and has authored or co-authored 300 scientific and other papers, and as a strong supporter of botanical art, has collaborated on several species monographs that appeared in *Flowering Plants of Africa (FPA)*.

Many of her publications deal with the taxonomy of a range of southern African succulents and of the 15 books she has authored or co-authored two are on aloes and one is on *Kalanchoe*. She was awarded the Rudolf Marloth Medal of the Botanical Society of South Africa for her work towards popularising the flora of South Africa.

She is celebrated in a number of plant names, including the Malagasy alooid genus *Aloestrela* that was treated and illustrated as Plate 2122 in volume 55 of *FPA*. It is fitting that the 68th volume of this journal is dedicated to Estrela, who co-authored several of the contributions found in its pages.





PLATE 2381 *Aloe labiaflava*

*Aloe labiaflava*

Asphodelaceae: Aloioideae

*South Africa*

***Aloe labiaflava*** Groenewald in Tydskrif vir Wetenskap en Kuns 14: 58 (1936); Groenewald: 87, 104, 134, 139 [page not numbered], Map no. 11 (1941); Smith & Kloppe: 181 (2021).

Not many plant taxonomists and collectors of plant specimens habitually produced colour paintings of their finds. Rather, in the days before cameras became widely accessible and, especially prior to colour photography becoming affordable, taxonomists most often relied on the talents of botanical artists to illustrate their work. However, engaging an artist was expensive and required overcoming logistical challenges to provide them with fresh material that had not faded or wilted. Even well into the 20th century, publications in which novel taxa were described, or revisions and monographs presented, were seldom illustrated, and if they were, with only black-and-white line drawings quite often based on pressed herbarium materials.

After the present serial work, originally titled *The Flowering Plants of South Africa*, was initiated in 1920, taxonomists working at the then Department of Plant Industry, one of the forerunners of the present-day South African National Biodiversity Institute, were fortunate to have the accomplished South African-born botanical artist Cythna Lindenberg Letty (1895–1985) (Figure 1) at hand to produce colour plates for inclusion in the series. From 1927 Letty was employed under the direction of Dr Iltyd Buller Pole Evans (1879–1968) (Gunn 1971), but left in 1938 after marrying. Post World War II, in 1945, she returned to the Division of Botany and remained there until her retirement in 1966. Her remarkably prolific and high quality output, which includes 730 illustrations for *Flowering Plants of Africa* (FPA), as the series is now known, resulted in her receiving numerous awards that included an honorary L.L.D. conferred by the University of the Witwatersrand.

Frederick Ziervogel van der Merwe (10 December 1894, Britstown, Northern Cape Province–2 January 1968, Claremont, Cape Town, Western Cape Province, South Africa) (Figure 2), the artist who prepared the plate of *Aloe labiaflava* published here, also collected the herbarium material on which Groenewald (1936) based the name. Van der Merwe was a medical inspector of schools in the then Transvaal and Natal provinces of South Africa and an amateur botanist, the latter categorisation considered a badge of honour by many non-academically trained plant enthusiasts in South Africa (Verdoorn 1966; Gunn & Codd

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PLATE 2381.—Coloured plate, dated 1 September 1935 and held at Herb. PRE, of which the corresponding components (habit, bud and flower, leaf and frontal view of flower mouth) agree with those in the black-and-white line drawing in Groenewald (1936: unnumbered page opposite p. 58), the protologue of the name *Aloe labiaflava*. 1, habit,  $\times 0.1$ ; 2, raceme,  $\times 0.75$ ; 3, aberrant flower [Afrikaans text written on the plate states: ‘afwykende blom: ligter as gewoonlik, meer oop, smaller buis’. English: aberrant flower: lighter coloured than usual, more open, narrower tube],  $\times 0.7$ ; 4, terminal portion of leaf in winter,  $\times 0.5$ ; 5, flower bud,  $\times 0.7$ ; 6, flower,  $\times 0.7$ ; 7, frontal view of the mouth of the flower,  $\times 0.7$ . Voucher specimen: F.Z. van der Merwe 100, lectotype of the name *A. labiaflava*, designated by Smith & Kloppe (2021), in National Herbarium (PRE), Pretoria. The name *A. labiaflava* was epitypified on G.F. Smith 1120, which is held in H.G.W.J. Schweickerdt Herbarium (PRU), Pretoria. Artist: F.Z. van der Merwe.



FIGURE 1.—Cythna Lindenberg Letty (1895–1985).



FIGURE 2.—Frederick Ziervogel van der Merwe (1894–1968).

1981; Glen et al. 1995). Van der Merwe was also a philanthropist and arranged holiday camps at the coast for children in need (Payne 1968).

In his professional capacity Van der Merwe published a glossary of Afrikaans medical terms and a medical dictionary. He also had an exceptional interest in identifying South African sheet music, specifically its collection and preservation. After his death his vast collection was bequeathed to the University of Pretoria where it is still maintained through a grant left by Van der Merwe. This collection is regarded as the largest and most comprehensive collection of South African sheet music in the world (Gunn & Codd 1981; Clarke & Charters 2016; <https://library.up.ac.za/c.php?g=1206269&p=8880654>).

Van der Merwe is known to have provided his novel aloe collections to Barend [Ben] Hermanus Groenewald (1905–1976), at the time a teacher at a high school in Polokwane (then Pietersburg), Limpopo Province, South Africa, for description during the 1930s (Anonymous 2010; Klopper et al. 2013), a contribution recognised by Reynolds (1950) in his list of ‘South African [*Aloe*] botanists since 1865’. It has been speculated that as an employed school inspector, Van der Merwe did not want to be seen describing new species of *Aloe* (Glen et al. 1995). However, it is possible that he wanted more simply to avoid the territorial disputes inherent in aloeology in the 1930s, especially with Harold Basil Christian (1871–1950) at the time active in Zimbabwe and other south-tropical and tropical African countries, and Reynolds in southern Africa south of the Limpopo River. Van der Merwe hesitated for many years before himself publishing any taxonomic articles based on his extensive field experience and when he did it was in another section of the broader ‘*Liliaceae*’, i.e., in

what is today recognised as the subfamily Hyacinthoideae of the Hyacinthaceae. Over a five-year period from the early 1940s Van der Merwe described 24 new taxa, including the new genera *Resnova* Van der Merwe and *Schizocarphus* Van der Merwe, with the majority of his protologues appearing in this very publication series. Van der Merwe published over 30 contributions in the *FPA* series, with the vast majority being on hyacinthoid species, and oddly with none illustrated by himself, despite his obvious artistic talent. Volume 24 (published in 1944) was dedicated to Van der Merwe to acknowledge his keen general interest in the South African flora over a period of many years, especially in recognition of his studies on the genus *Scilla*, and the numerous species described by him in the pages of the *FPA* series.

Following Van der Merwe's discovery of *Aloe labiaflava* (Figure 3) in 1935 and the aloe's description by Groenewald in 1936, the species was accepted for about 14 years. However, Reynolds (1950), in his monograph on the aloes of South Africa, interpreted this species '...as a cross between *A. davyana* and *A. longibracteata*'. All three species are placed within *A. sect. Pictae* (Salm-Reifferscheidt-Dyck 1837), an infrageneric group in *Aloe* commonly referred to as the 'maculate aloes' (Van Wyk & Smith 2014).



FIGURE 3.—Plants of *Aloe labiaflava* usually develop a single rosette only, with a rosette often producing only a single inflorescence during a flowering season. Photograph: G.F. Smith.

Reynolds (1950) regarded both *Aloe davyana* Schönland (1905) and *A. longibracteata* Pole-Evans (1915) as accepted species, but Glen & Hardy (1987) subsequently included *A. davyana* under *A. greatheadii* Schönland (1904) at the rank of variety, as *A. greatheadii* var. *davyana* (Schönland) Glen & D.S.Hardy, and simultaneously included *A. longibracteata* in the synonymy of *A. greatheadii* var. *davyana*. However, Smith et al. (2020) recently reinstated *A. davyana* at the rank of species, whilst also recognising the more northern element, *A. greatheadii*, at species rank. Smith et al. (2021) thereafter also reinstated *A. davyana* var. *subulifera* Groenew. (Groenewald 1939), a further entity that Glen & Hardy (1987) included in the synonymy of *A. greatheadii* var. *davyana*. More recently, Smith (2022) described the nearly red-flowered *A. davyana* var. *magdae* Gideon F.Sm. from the southern parts of the distribution range of *A. davyana*. These reinstatements and description have allowed for a reassessment of the status of *A. labiaflava*, which Smith & Klopper (2021) showed warrants recognition as an accepted species. They argued that *A. labiaflava* is not of hybrid origin [*A. davyana* × *A. longibracteata*], but that it is rather a distinct species requiring



FIGURE 4.—*Aloe labiaflava* usually grows as solitary specimens. In the cold winter months the leaves die back to yield small, squat rosettes. Photograph: G.F. Smith.

reinstatement. Although *A. davyana* var. *davyana* occurs sympatrically with *A. labiaflava*, it cannot, based on reproductive morphological evidence, be confused with *A. labiaflava*. Further, Reynolds' other putative parent, *A. longibracteata*, has not been found within the limited distribution range of *A. labiaflava*, which argues against it contributing parentage.

Like *Aloe longibracteata*, *A. labiaflava* usually grows as solitary specimens (Figure 4), while the autonymic variety of *A. davyana*, with which *A. labiaflava* grows sympatrically, is most often found in clusters of usually not more than four rosettes that arise from a single rootstock. Relative to *A. davyana* var. *davyana*, *A. davyana* var. *subolifera* forms large, suckering clumps, and has shorter, smaller leaves resulting in narrower rosettes, longer, laxer inflorescences, and shorter flowers, and its flowers are generally lighter in colour – almost white in some instances.

In the case of *Aloe labiaflava*, plants almost invariably produce only a single, often unbranched, inflorescence each flowering season. At maturity, plants of *A. davyana* usually produce up to three inflorescences simultaneously or successively, while plants of *A. longibracteata* usually successively produce two inflorescences (Smith & Klopper 2022). A distinctive feature of the flowers of the appropriately named *A. labiaflava* is that the apical third of the perianth is whitish yellow to golden yellow (Figure 5). The rest of the flower is bright orange to bright reddish orange. In contrast, flower colour in *A. davyana* var. *davyana* is in general duller, ranging from pale flesh-pink to dull brick-red with contrasting greenish to



FIGURE 5.—The apical third of the perianth of *Aloe labiaflava* is whitish yellow to golden yellow. The mouth of the perianth is distinctly flared open. Photograph: G.F. Smith.

greyish, longitudinal stripes (Figure 6). *Aloe longibracteata*, on the other hand, has flowers that are usually strawberry-pink to peach-red, with the mouth much paler than the rest of the flower, being yellowish. The interior of the perianth mouth of both *A. davyana* var. *davyana* and *A. longibracteata* can present as a light shade of yellow, although the exterior of the perianth is never yellow. In addition, the perianth segments of the flowers of *A. labiaflava* are distinctly flared, whilst those of *A. davyana* var. *davyana* and *A. longibracteata* flare only slightly, or not at all. *Aloe davyana* var. *subolifera* has a more westerly distribution range than *A. labiaflava* and does not occur anywhere near localities for the latter species.

Whereas several maculate aloes have very wide natural geographical distribution ranges, *Aloe labiaflava* is, as far as presently known, restricted to a small area around Kwa-Mhlanga and Gembokspruit in western Mpumalanga Province, South Africa (Figure 7). The species typically grows on rocky outcrops in sparse to medium-dense grassland.

**Description.**—Plants small, low-growing, solitary, rarely once-branched from the base, rosette erect, up to (100–)200 mm tall. *Stem*  $\pm$  absent, short, simple and thickened basally



FIGURE 6.—Flower colour in *Aloe davyana* var. *davyana* (inflorescence on the left) is duller, ranging from pale flesh-pink to dull brick-red, than that of the bright orange to bright reddish orange-flowered *A. labi-aflava* (inflorescence on the right). Photograph: G.F. Smith.

if present, clothed in persistent, twisted, dried leaves. *Leaves* very densely rosulate, at first erect, then horizontally spreading, 50–150 × 70–100 mm, deltoid-lanceolate, dull greenish to purplish blue to glaucous, abaxially pale green, faintly white-spotted, longitudinally purple-lined, lines narrow, somewhat confluent, adaxially more densely white-spotted, purple-lined but less so than abaxially, white spots ± oblong, sometimes arranged in interrupted, wavy transverse bands, texture smooth; margins shiny orange-brown to shiny dark brown, dentate; teeth prominent, ± 4–6(–9) mm long, 3–5(–9) mm apart, very pungent, deltoid, variously curved towards leaf base or more rarely straight, shiny-brown, apex yellowish. *Inflorescence* usually only one produced per season, unbranched raceme or 2- to 4-branched panicle, 0.6–0.8 m high, erect, branched at or below middle, branches erect at narrow angle from peduncle; peduncle stout, lacking sterile bracts below racemes, panicle branches subtended by prominent sterile bracts of 25–40 mm in length, drying rapidly, dull light brown to creamy white, irregularly deltoid to lanceolate-triangular, distinctly longitudinally dark brown lined. *Raceme* narrowly cylindrical, somewhat tapering upwards, 100–300 × 40–60 mm, at anthesis, usually rather densely flowered; buds erect to erectly spreading, flowers pendulous at anthesis. *Floral bracts* 15–20 mm long, much narrower than sterile bracts, as long as or longer than pedicels, prominent, narrowly lanceolate, variously twisted, drying

rapidly, light brown to creamy white. *Pedice*l (5–)10–15(–20) mm long, orange to reddish orange when young, light green with age. *Perianth* uniformly orange to reddish orange in bud, apex green-tipped at anthesis, bright orange to bright reddish orange for proximal two-thirds, whitish yellow to golden yellow in distal third,  $\pm$  30 mm long, 6–7 mm wide across ovary, narrowed above ovary to yield small bulbous base, distinctly enlarged towards mouth, middle  $\pm$  cylindrical,  $\pm$  straight to down-curved to horizontally spreading; apex of segments distinctly flared, outer segments free for half of their length; stamens exserted for up to 3–6 mm, uniformly light yellowish white, filaments filiform-flattened; ovary 6–7  $\times$  2–3 mm, light green; style well-exserted, uniformly light yellow; stigma minute, very slightly capitate, yellowish. *Fruit* a trilocular, loculicidal capsule, 15–20  $\times$  8–10 mm, dull mid-green to purplish green, dry remains of perigone persistent for long time. *Seed* not seen. *Chromosome number*: unknown. Plate 2381.

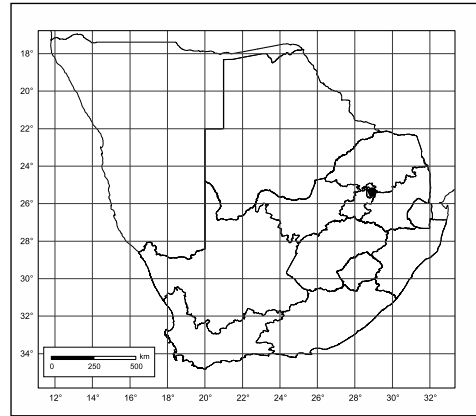


FIGURE 7.—Known natural geographical distribution range of *Aloe labiaflava* in South Africa.

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PLATE 2382 *Aloiaampelos tenuior* var. *ernstii*

*Aloiampelos tenuior* var. *ernstii*

Asphodelaceae: Aloooideae

South Africa

***Aloiampelos tenuior*** (Haw.) Klopper & Gideon F.Sm. **var. *ernstii*** Gideon F.Sm. & Figueiredo in Phytotaxa 571(1): 94 (2022).

During a ca. 30-year period, between 1950 and 1982, the benchmark book on the aloes of South Africa of Gilbert Westacott Reynolds (1895–1967) saw four editions, apart from the first one, that were published by two different publishers (Reynolds 1950, 1969, 1970, 1974, 1982) (see Walker 2010 for a discussion of the work of Reynolds on *Aloe* L.). The second edition, which was reprinted within a year of its first printing (in 1970), up to the fourth and final edition, all appeared within just more than a decade and no doubt played a pivotal role in stimulating what was eventually referred to as the ‘aloe craze’ of the 1960s and 1970s that manifested among the gardening fraternity of the country (Klopper et al. 2013). In the 1970s, interest in *Aloe* L. was further fuelled by the books of Judd (1967), Jeppe (1969) and Bornman & Hardy (1971).

At the time, people went to extraordinary lengths to acquire aloes for their gardens, with at least one surviving report noting that Hendrik Kruger of Pietersburg [now Polokwane] in the northern, Limpopo province of South Africa travelled 9 600 km on a motor-cycle – his only means of transport – to collect 227 different species of *Aloe* (Anonymous 2019). It was, inter alia, noted that he once travelled with a 3 m tall specimen of *A. speciosa* Baker on his shoulder; the plant weighed 45.4 kg. It was not stated whether he obtained the specimen from the natural geographical distribution range of *A. speciosa*, which is about 1 200 km south of Polokwane. However, Anonymous (2019) did note that Mr Kruger could not use the arm with which he held on to the aloe for a week!

In addition to the work of Reynolds and others on *Aloe* from the 1930s to the 1960s, in the 1950s Arthur ‘At’ Koeleman (1915–1994) initiated the large-scale hybridisation of aloes that resulted in the initially slow but eventually steady increase in aloe cultivars with considerably improved horticulturally desirable characters reaching the market place (Krüger 1983; Smith 1996; Smith & Figueiredo 2015).

However, the ‘aloe craze’ did not last. Along with large numbers of wild-collected aloes, the insects that feed on aloes – often immensely destructively so – were also introduced into gardens and many collections succumbed to, among others, the aloe snout weevil. During the 1980s and up to the mid-1990s, aloes fell somewhat out of favour as garden subjects, with interest in South African aloes as garden subjects in general only being revived following publication of Van Wyk & Smith (1996 [as well as the 2003 and 2014 editions]) and by then increasingly successful breeding and availability of exquisitely beautiful and highly floriferous, and in some instances, more pest-resistant, cultivars from a new



FIGURE 1.—As a backdrop planting, *Aloiampelos tenuior* var. *tenuior* 'Gamtoos', a yellow-flowered cultivar, serves as a textural foil for any planting in front. Scrambling aloes have a clumping habit which makes them a good choice for growing in a medium-sized or large garden. Photograph: G.F. Smith.

generation of breeders, especially Andy de Wet and Quinton Bean, and Leo Thamm (Smith & Figueiredo 2015).

In South Africa, species of aloe, today included in the genera *Aloe*, *Aloiampelos* Klopper & Gideon F.Sm., *Aloidendron* (A.Berger) Klopper & Gideon F.Sm. and *Kumara* Medik., are currently again experiencing an unprecedented level of interest as they steadily increase in popularity as garden subjects – waterwise ones to boot. Arguably the most popular species used in large-scale gardening and landscaping projects are *Aloidendron barberae* (Dyer) Klopper & Gideon F.Sm. (*mikaalwyn* [Afrikaans], tree aloe) as an accent tree, *Aloe arborescens* Mill. (*kransaalwyn* [Afrikaans], krantz aloe) as a large, hedge-forming shrub or shrub-like tree, and *A. cooperi* Baker (*grasaalwyn* [Afrikaans], Cooper's aloe) as an increasingly popular element of the South African version of 'meadow gardens'.

A further very popular aloe among gardeners is *Aloiampelos tenuior* (Haw.) Klopper & Gideon F.Sm. (*heuningaalwyn* [Afrikaans], fence aloe) (Onderstall 1981: 94). This species has three distinct flower-colour forms, with the yellow one – represented by several varieties – being somewhat more popular than the red one, and as discussed here, with the orange one today being almost unknown in cultivation. The yellow-flowered forms, such as the cultivar *A. tenuior* var. *tenuior* 'Gamtoos' (Figure 1) generally grows and flowers more prolifically than the red- and orange-flowered variants. Some variants of the species are very cold tolerant and even when the above-ground stems get frosted down to ground level every winter, they generally and often quite rapidly resprout in spring. *Aloiampelos tenuior* is very easy to cultivate because all that is required is to stick a stem into the ground where it is intended to grow. As a reminder of the thicket vegetation in which at least some of the forms of this species, and its relatives, occur, they also thrive in quite heavy, if ideally dappled, shade, especially when young.

The subject of this paper is the orange-flowered variant of *Aloiampelos tenuior*, which was recently described as *A. tenuior* var. *ernstii* Gideon F.Sm. & Figueiredo (Figure 2). In the most recent taxonomic treatment of *A. tenuior*, which was published in the pages of *Flowering Plants of Africa* (Van Jaarsveld & Visagie 2021), this variable species – in terms of both vegetative and reproductive morphology – was recognised as encompassing four varieties, apart from the autonymic one. That treatment recognised: (1) *A. tenuior* var. *decidua* (Reynolds) Van Jaarsv.; (2) *A. tenuior* var. *densiflora* (Reynolds) Van Jaarsv.; (3) *A. tenuior* var. *rubriflora* (Reynolds) Van Jaarsv.; and (4) *A. tenuior* var. *viridifolia* (Van Jaarsv.) Van Jaarsv.



FIGURE 2.—Stem and flower characteristics: a, thin, weak stems of *Aloiampelos tenuior* var. *ernstii* are typical of those of the other varieties recognised in the species; b, flowers of *A. tenuior* var. *ernstii* are orange rather than yellow or red as in other varieties recognised in the species. Photographs: G.F. Smith.

*Aloiampelos tenuior* var. *ernstii* is the fifth variety recognised in the species. With the exception of the red-flowered *A. tenuior* var. *rubriflora*, three of the other varieties are predominantly yellow- or yellowish green-flowered, with *A. tenuior* var. *ernstii*, in contrast, having orange flowers.

Some 40 to 50 years ago the orange-flowered variant of the species was very common in cultivation in many parts of South Africa. However, it is nowadays not often seen in gardens and it seems to have been one of the casualties of the collapse of the ‘aloe craze’ of the 1970s and the subsequent decrease in the popularity of aloes in the subsequent two decades. With the wide availability of very floriferous material of *Aloiampelos tenuior* var. *tenuior*, i.e., of the typical, yellow-flowered one, gardening trends have apparently selected against cultivating the orange variant, and to a lesser extent also the red-flowered variety.

Trends and fashions ebb and flow in horticulture, with domestic and amenity gardening having seen significant changes during the past centuries as some plants decreased or increased in popularity (see Grimaldi & Robyns (1980) and Lucas (1983) for general discussions, and Mabey (2016) on the fern craze that raged in, inter alia, the United Kingdom during the 19th century). Adopting the latest trends almost inevitably results in some well-known species, or cultivars, falling out of favour, with these plants eventually disappearing from our gardens. Where referring to rejuvenating the rose garden at Waddesdon Manor, Aylesbury, Buckinghamshire, United Kingdom, one of the famed Rothschild gardens that was created at the end of the 19th century, this one by Baron Ferdinand de Rothschild, it was noted that it will require several new varieties because, ‘...many of the original cultivars have disappeared’ (Rothschild et al. 2004). It was also noted that, when planning a newly added butterfly garden for Waddesdon Manor, ‘...many of the new horticultural varieties of herbaceous plants have lost both their scent and their attractive nectar and a great effort will be made to obtain seed and plants of the more primitive “cottage garden” varieties’, and, similarly, that the ‘...original ice plant (*Sedum*) is not easy to find’ (Rothschild et al.



FIGURE 3.—The ‘original ice plant (*Sedum*)’ mentioned by Rothschild et al. (2004) as not easy to find when renovating a garden at Waddesdon Manor, United Kingdom, likely referred to *Sedum fabaria* (Crassulaceae), the currently accepted name of which is *Hylotelephium telephium*, a variable northern hemisphere *plakkie*. Photograph: G.F. Smith.

2004). Reference to a ‘sedum’ is likely to the crassuloid leaf succulent *Sedum fabaria* W.D.J.Koch, which is today usually treated as belonging in the synonymy of *Hylotelephium telephium* (L.) H.Ohba, a remarkably variable northern hemisphere species (R. Stephenson, personal communication; see Praeger 1921) (Figure 3). Today the vernacular name ice plant is widely applied to representatives of the Aizoaceae, a family of predominantly southern African leaf succulents that is unrelated to the Crassulaceae.

The popularity of some garden plants certainly increased or decreased as distant lands were explored in previous centuries, which gave wealthy plant collectors in the United Kingdom and continental Europe unprecedented access to novelties hardly dreamed of before (see for example [www.nationaltrust.org.uk/features/potted-history-of-houseplants-in-our-houses-and-collections](http://www.nationaltrust.org.uk/features/potted-history-of-houseplants-in-our-houses-and-collections)). However, to this day, gardening fashions change often and regularly, and for many gardeners there is always the challenge to be the first to successfully grow a new horticultural introduction, or to start a trend that becomes fashionable. For example, an increasingly widespread trend in South Africa is to use indigenous plants

when starting, or redeveloping, a garden. This is an appropriate development that ensures that gardens are becoming more sustainable and environmentally friendly.

In other cases, the frequency at which some species are found in gardens decline because they prove to be rather challenging to grow and costly to maintain, while others are displaced simply because new (which for many people means ‘better’) selections of well-known favourites become available. In this regard, new cultivars of species of *Zantedeschia* K.Koch (*varkore* in Afrikaans or calla lilies), *Rosa* L. (roses), *Viola* L. (violets, especially the fragrant ones), and numerous others, have displaced what have come to be known, rather derisively, as the ‘common garden varieties’ of these same, and other, genera.

It is unlikely that *Aloiampelos tenuior* var. *ernstii* is a hybrid between the red and yellow forms that will, through introgression, eventually revert to the red and yellow variants. The offspring of aloe hybrids generally often show considerable heterosis (Smith & Figueiredo 2015), which is not evident in *A. tenuior* var. *ernstii*. However, the general growth form of most species of *Aloiampelos* has been used in creating some excellent hybrids for the garden. For example, the growth form, as well as the inflorescence and flower morphologies

of the cultivar *Aloe* 'Little Easy' (see De Wet Plant Breeders [no date: 23]), are very much reminiscent of those of representatives of *Aloiampelos* (Figures 4 and 5).

The hybrid between *Aloe arborescens* and *Aloiampelos tenuior* belongs in the nothogenus  $\times$ *Aloiampaloe* G.D.Rowley (see Rowley 2014). The bright red- to red-orange-flowered inflorescences of the hybrid offspring are sparser-flowered than in *Aloe arborescens* (Figures 6 and 7). This nothospecies is beginning to attract horticultural attention.

Material of *Aloiampelos tenuior* var. *ernstii* was collected by Reynolds who sent the material to the Royal Botanic Gardens, Kew, in England. A herbarium specimen was prepared in 1951 and deposited at Kew Herbarium. The specimen lacks information on the collecting locality, being only labelled as originating from South Africa. The variety has not been recollected since then and it is not known if it still occurs in the wild. For this reason no distribution map can be presented here.



FIGURE 4.—The growth form and stem morphology of the popular cultivar *Aloe* 'Little Easy' are similar to those of representatives of *Aloiampelos*. Photograph: G.F. Smith.

Including a plate of *Aloiampelos tenuior* var. *ernstii* in volume 68 of *Flowering Plants of Africa* also serves to celebrate the 70th birthday of Dr Ernst Jacobus ('Ernst') van Jaarsveld (1953–), after whom the variety was named. Ernst has a long-standing interest in the South African flora and succulents in particular, and is presently involved in establishing a succulent plant collection at Babylonstoren Farm, near Simondium, Western Cape. Dr Van Jaarsveld was employed by the South African National Biodiversity Institute for more than 40 years and has inspired and trained scores of emerging botanists and horticulturalists.

**Description.**—Perennial, herbaceous, tangled, succulent shrub of 0.75–1.00 m tall. *Stems* clumped, slender, (0.50–)0.75–1.00 m long, 5–10 mm diameter, branched low down or higher, erectly spreading or scandent to recurved or decumbent, mostly without persistent dried leaves. *Roots* cylindrical, 5 mm in diameter. *Leaves* rosulately and widely cauline-dispersed, erectly spreading to down-curved, papery when dry, dull light green to mid-green, without spots, linear-lanceolate to linear-attenuate, upper surface slightly concave to canaliculate, lower surface convex, texture smooth, tapering to apex, 70–190 mm long, 9–11 mm broad at base, basally sheathing; sheath obscurely to distinctly green-lineate, not auriculate, 5–20 mm long; margin same colour as blade, not cartilaginous, with minute, white teeth, up to 0.5 mm long, 1–5 mm apart. *Inflorescence*



FIGURE 5.—The cultivar *Aloe* 'Little Easy' has bicoloured inflorescences (orange buds and yellow open flowers) that are more robust and densely flowered than most variants of the horticulturally popular *Aloiaimpelos tenuior*. Photograph: G.F. Smith.

1–3, borne simultaneously or successively, 100–120 mm tall, rarely once-branched, branch arcuate-erect. *Peduncle* 60–70 mm long, 3–4 mm broad at base, basally plano-convex, cylindrical above, light green, lacking a white, powdery bloom; sterile bracteate lower down; sterile bracts up to 5, deltoid-triangular low down, long-attenuate, hair-like above, 3–6 mm long, straw-coloured, scarious, 1–3-nerved. *Racemes* cylindrical, 50–80 × 40–50 mm; buds erect to suberect, flowers horizontal to drooping when mature. *Floral bracts* tapering long-attenuate and hair-like from a deltoid triangular base, not amplexicaul around pedicel, 3–4 × 1.0–1.5 mm, straw-coloured, papery, 3- or 4-nerved, central nerve dark brown, prominent. *Pedicels* 3–4 mm long, light green. *Flowers* actinomorphic, unscented, nectariferous. *Perianth* orange, yellow towards tip, tip extremity green in bud and when mature, not pruinose, 12–15 mm long, rounded at base, ± 3 mm across ovary, enlarging to 4 mm towards wide open mouth, cylindrical,



FIGURE 6.—The hybrid between *Aloe arborescens* and *Aloiaimpelos tenuior*, figured here, correctly belongs in the nothogenus ×*Aloiaimpaloe*. The rosettes of this shrubby species are intermediate between those of its two parents. Photograph: G.F. Smith.

tubular-cymbiform; outer segments lorate, free for  $\pm 4$  mm, free portion centrally green, borders yellow, acute, blunt-tipped, segment margins straight, tips slightly flared open; inner segments  $\pm$  same size as outer segments, with yellow border and slightly more obtuse apex, free for  $\pm 4$  mm. Stamens with cylindrically thread-like, light yellow, basally inserted filaments, 12–15 mm long, all 6 of  $\pm$  equal length, prominently exerted for 2–3 mm; anthers small, 1–2 mm long, yellow, fading brown, versatile. Ovary 3–4 mm long,  $\pm 2$  mm in diameter, light yellow; style as long as or slightly longer than stamens, minutely capitate, with small stigma, exerted 1–2 mm. Fruit not seen. Seeds not seen. Chromosome number unknown. Plate 2382.

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Ray Stephenson, United Kingdom, is thanked for expressing a view on the identity of the 'original ice plant' that has apparently fallen out of horticultural favour in parts of the United Kingdom.



FIGURE 7.—The bright orange-flowered inflorescences of the hybrid between *Aloe arborescens* and *Aloiampelos tenuior* are sparsely flowered, a character inherited from *A. tenuior*. It is not known whether the *Aloiampelos* parent represented the yellow- or red-flowered variant. Photograph: G.F. Smith.

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PLATE 2383 *Xerophyta burrowsiorum*

*Xerophyta burrowsiorum*

Velloziaceae

South Africa

***Xerophyta burrowsiorum*** D.McMurtry & S.Burns sp. nov. differs from the equally dwarf *X. humilis* (Baker) T.Durand & Schinz by its naked (not densely glandular) ovary; cremnophytic (not psammophytic) habitat; and by having its crowns above (not below) ground. It differs from *X. elegans* (Balf.) Baker by its ovary with rounded angles (rather than with sharp angles and wings); columnar (not clavate) stigma, stigma that overlaps (rather than stands clear of) anthers, stamens adnate to adaxial tepal surface (rather than adnate to roof of ovary); and much smaller and narrower [(9–)40(–113) × (2.0–)3.8(–6.5) mm, not (100–)150(–200) × 13–18 mm] leaves (Figure 1).

TYPE.—SOUTH AFRICA, Mpumalanga: Lydenburg District, Graskop, below Lisbon Falls, Farm Ledovine 507KT, on boundary of Blyde Plantations, 1 260 m (2430DD), 25 October 2008, J.E. Burrows 10620 (J, holotype; PRE, isotype).

[Note: although the label states Ledovine, the collection was made just east of the boundary of Ledovine, on the farm Berlyn 506KT.]

Domenico (Domingos) Agostino Vandelli (1735–1816) was an Italian botanist who had taken a teaching post in Lisbon and had been granted his degree in Natural Philosophy and Medicine from the University of Padua in 1761 (Moraes 2019). A dedicated and methodical collector of natural history specimens, he accumulated a substantial private museum that was scientifically significant enough to later be accepted as the inaugural core of the Museum of Coimbra University, Portugal (Cardoso 2003). At age twenty-nine he had been appointed to a teaching post at the Royal College of the Nobility in Lisbon. His progress was rapid and within eight years he had founded the first botanical garden in Portugal, and it was to this garden in Lisbon that many specimens of newly discovered plants from Portuguese colonies were methodically and often laboriously shipped (Cardoso 2003). An important collector in Brazil and a contemporary of Vandelli was Velloso Joaquim de Miranda (Urban 1906) whose pressed specimens would ultimately reach Vandelli's desk for critical botanical deliberation (Moraes 2019). One can only imagine the awe as Vandelli perused the overwhelming number of taxa, all new to science. In 1788, Vandelli authored the genera *Vellozia* and *Barbacenia* (Mello-Silva 1991) placing *Vellozia* in his Class 12, *Icosandria monogynia* (twenty stamens and one ovary) and *Barbacenia* in Class 6, *Hexandria monogynia* (six stamens and one ovary). These were the first of the genera currently included in family Velloziaceae to be described. Vandelli's choice of names for his two new genera was influenced, firstly by the sobriquet Velloso (Clarke & Charters 2016), and possibly because one of Miranda's specimens had been collected near the town of Barbacena, Minas Gerais State, which lies 180 km north of Rio de Janeiro.

The genus *Xerophyta* was established in 1789 by the prolific savant, Antoine Laurent de Jussieu (1789), in his *Genera plantarum* (Baker 1875). He was born in Lyon, France, on

PLATE 2383.—1, habit, × 2; 2, flower, × 2.5; 3, fruit, × 3. Voucher specimen: Burrows 10620 previously in Buffelskloof Nature Reserve Herbarium (BNRH), Lydenburg, now in C.E. Moss Herbarium (J), Johannesburg. Artist: Sandra M. Burrows.



FIGURE 1.—Comparison of vegetative features (leaf size) of different *Xerophyta* species cultivated under the same conditions: top, *X. humilis*; bottom left, *X. elegans*; bottom right, *X. burrowsiorum*. Photograph: D. McMurtry.

12 April 1748 and died on 17 September 1836 in Paris (Burdet 1976) after an acclaimed academic life. By the last quarter of the 18th century the Mascarene Islands had been claimed as French possessions and, hence, when a specimen of a strange fibrous-stemmed plant was collected on Madagascar sometime between October 1770 and January 1771 by the indefatigable naturalist Philibert Comerson (1727–1773), his pressed voucher naturally came to the attention of Jussieu in Paris, who erected the genus *Xerophyta* to accommodate this distinctive Madagascan species (Jussieu 1789). He placed his new genus in his Class 3 Order 5, Plantae Monocotyledones Stamina Perigyna, Bromeliales ananas (monocotyledons with stamens around the ovary, bromeliads or the pineapples).

It was not until 1824 that Martius combined *Xerophyta* and *Vellozia* under the younger name *Vellozia* (as *Vellosia*) and treated the genus as part of the Haemodoraceae (Martius 1824). In 1830, David Don initially suggested that ‘*Vellosia*’, *Barbacenia* and *Xerophyta* would be better placed in the Hypoxidaceae (then known as Hypoxideae) than the Bromeliaceae, and then on the basis of additional information he obtained from the seed coat, he suggested they should be placed in a family of their own, intermediate between the Bromeliaceae and the ‘Hypoxideae’, but he did not use the name Vellozieae or Vellosieae. Endlicher (1837) treated *Barbacenia* and ‘*Vellosia*’, including *Xerophyta*, as Vellozieae within the Haemodoraceae, and in his treatment Meisner (1836–1841) followed suit. Baker (1883) treated *Vellozia* and *Barbacenia* as a tribe, Vellozieae, under the Amaryllidaceae (as Amaryllideae). Seubert (1847) was the first to recognise the family Velloziaceae when he treated *Barbacenia* and ‘*Vellosia*’ as a family under the name Vellosieae. Agardh (1858) also recognised the Velloziaceae as a family, was the first to use the spelling Vellozieae at family level, and he provided a diagnosis against the Haemodoraceae – the spelling with a ‘z’ in this publication is conserved (Appendix IIB in Turland et al. 2018). Drude (1886) was the first to use the name in the form Velloziaceae and he was followed by Pax (1888) and most subsequent authors.

Whether the African and Madagascan species of the family have been treated as *Vellozia* or *Xerophyta* has depended on which characters (number of stamens, morphology of the stamens, morphology of the stigma or degree of fusion of the perianth) have been regarded as most important in the circumscription of the genera within the family (Mello-Silva 1991). When Endlicher (1837) treated the Velloziaceae in his *Genera plantarum*, two African species of *Xerophyta*, *X. pinifolia* Lam. ex Poir. and *X. madagascariensis* J.F.Gmel. (now a synonym of *X. pinifolia*), had been described from Madagascar. In his system, these two species would

have been transferred to '*Vellozia*'. Baker (1875) provided a synopsis of the 12 African species of Velloziaceae (nine of which he described in that publication) and treated them in *Xerophyta*, however, he also indicated that eight Brazilian species belonged to *Xerophyta* as he had defined the genus. In 1878 Baker described another four African species in *Xerophyta* and a further two from Madagascar in 1882. Ridley (1883) described another species of *Xerophyta* from Madagascar in the same year that Baker (1883) provided an account of Vellozieae (as a tribe of the Amaryllideae) in Bentham and Hooker's *Genera plantarum* and there indicated that all the African and Madagascan species were to be treated as a section within *Vellozia*. Pax (1888) placed the genus *Xerophyta* as a section of *Barbacenia*, although he did not make all the new combinations, as he was working at family level. Durand and Schinz (1895) treated the African species in the genus *Xerophyta* in the tribe Xerophyteae in the Amaryllideae. In *Flora capensis* (Baker 1896) and *Flora of tropical Africa* (Baker 1898), Baker treated the African members of the Velloziaceae in the genus *Vellozia*. This approach was followed by Greves (1921), but not by Coetzee et al. (1973) who treated the South African species in the genus *Xerophyta*. Furthermore, Smith and Ayensu (1974) treated all Old World species in the genus *Xerophyta* and Behnke et al. (2013) did the same.

Balfour (1867a, b, c) provided a description for a new member of *Vellozia* to accommodate a plant that had been sent to him by H. Fox Talbot. He initially called it *Vellozia elegans* and added that, once more flowers were available to confirm various characters, he would elevate it to a new genus, *Talbotia*. In 1869 the species was depicted in Curtis's Botanical Magazine as '*Vellozia elegans* Oliver ex Balfour' wherein Hooker (1869) pointed out that Balfour had not stated how *Talbotia* differed from *Vellozia* and that it seemed that the existence of *Xerophyta* to accommodate African taxa of 'Vellozieae' had been overlooked. The recognition of *Talbotia* has remained controversial ever since. One unique character used by Dyer (1976) to distinguish *Talbotia* is the naked ovary. Using DNA sequences from five regions, Mello-Silva et al. (2011) found that *Talbotia* was always sister to *Xerophyta* and that *Xerophyta* was monophyletic, whether or not *Talbotia* was included. In view of the shared characters of basally loculicidal capsules and hexaploidy and to maximise phylogenetic information and ease of identification, they recommended subsuming *Talbotia* into *Xerophyta*. This approach has been followed by Behnke et al. (2013) in the most recent revision of African Velloziaceae.

*Xerophyta burrowsiorum* was discovered on a Mpumalanga Plant Specialist Group outing that aimed to locate *Ledebouria parvifolia* S.Venter at its type locality, 'near Lisbon Falls, Farm Lisbon 531' (Venter & Edwards 1998). Although the *Ledebouria* was not found, a diminutive *Xerophyta* was spotted on a rocky dolomite outcrop with some low craggy cliffs. Photographs were taken (Figure 2), a herbarium specimen was prepared and a plant was cultivated at Buffelskloof nursery. On a subsequent trip in 2019 to collect flowering material, rock outcrops on an open north-facing slope to the south of the original collection were identified as promising *Xerophyta* habitat and a small colony of the dwarf species was located (Figure 3a), but only one flower was found. Another attempt to collect flowering material was made in February 2022. An east-facing colony (Figure 3b) was found and then an additional population growing on a west-facing dolomite cliff (Figure 4a) was spotted through binoculars because it was in full flower (Figure 4b). This colony comprises about 2 000 individuals. The four known localities each has a different aspect, making this new taxon appear generalist and adaptable in its choice of habitat orientation.



FIGURE 2.—The first plants of *Xerophyta burrowsiorum* that were discovered: a, habit of plants in crevitic habitat; b, side view of flower. Photographs: J.E. Burrows.

John Burrows initially identified this species as a member of *Talbotia* (then regarded as a genus separate from *Xerophyta*), because of its small size, but more importantly because the ovary and pedicel were completely devoid of glandular trichomes (Figures 2b, 5b) exactly like the naked ovary of *Talbotia elegans* Balf. (now *X. elegans*). Despite the glabrous ovary, this species lacks wings on the ovary, has stamens adnate to the tepals (Figure 5a) rather than to the roof of the ovary and has a columnar (Figure 5d) rather than clavate stigma, thus it is described as a species of *Xerophyta* rather than *Talbotia*, even although we would prefer to treat *Talbotia* as a separate genus.

*Xerophyta burrowsiorum* occurs at altitudes of around 1 260 m and is confined to crevices and narrow shelves of dolomitic outcrops and cliffs (Figures 2a, 3, 4) of the Malmani Dolomites (Norman & Whitfield 2006). After having explored all four known sites, a number of associated taxa were noted. They include true dolomite obligates like *Aloe alooides* (Bolus) Druten and *Kalanchoe crouchii* Gideon F.Sm. & Figueiredo, as well as *Catha edulis* (Vahl)

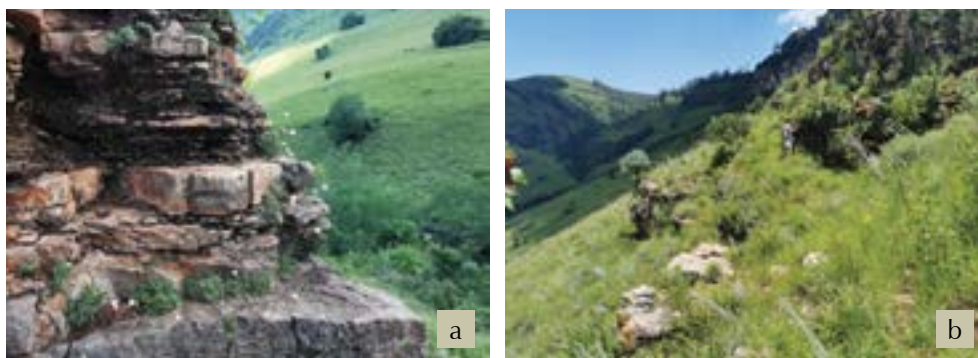


FIGURE 3.—*Xerophyta burrowsiorum*: a, plants located in 2019 on north-facing cliff face; b, east-facing habitat located in 2022. Photographs: D. McMurtry.



FIGURE 4.—*Xerophyta burrowsiorum*: a, west-facing habitat of plants located in 2022; b, plants in full flower accessed by Shane Burns in 2022. Photographs: D. McMurtry.

Forssk. ex Endl., *Crassula sarcocaulis* Eckl. & Zeyh., *Gymnosporia heterophylla* (Eckl. & Zeyh.) Loes., *Merwillia plumbea* (Lindl.) Speta, *Oxalis obliquifolia* Steud. ex A.Rich., *Pelargonium dolomiticum* R.Knuth, *Pellaea calomelanos* (Sw.) Link, *Plectranthus neochilus* Schltr., *Plectranthus strigosus* Benth., *Seemannaralia gerrardii* (Seem.) Harms, *Selaginella mittenii* Baker, *Steganothaenia araliacea* Hochst. and *Tetradenia brevispicata* (N.E.Br.) Codd. A second species of *Xerophyta* co-occurs in the area, but in open rocky grassland and on the top edges of the outcrops, rather than on the cliff faces. It is a clump-forming, tufted perennial with glandular pedicels and ovaries, and leaf apices that dry to a distinctive grey that reflects sunlight. It is most likely related to *X. viscosa* Baker. Two individuals that were otherwise like *X. burrowsiorum* were slightly larger vegetatively and had glands on the pedicel, ovary and tepals (Figure 6), as does the sympatric *X. viscosa*-like taxon, and these are probably hybrids.

*Xerophyta* refers to the ability of members of this genus to grow in areas that are intermittently extremely dry and they have the ability to revive after drying out (Clarke & Charters 2016). The specific epithet, *burrowsiorum*, honours the proficient husband and wife team of John and Sandie Burrows. Besides many other achievements, including more than 16 000 herbarium specimens, numerous papers on a wide variety of botanical subjects, line drawings for books and papers, and authorship of well-received botanical books (Glen & Germishuizen 2010; Oosthuizen & Balkwill 2019), their outstanding achievements as longstanding key members and substantial contributors to the 'Mpumalanga botanical brigade' and their protracted and loyal tenure of the 1 500 ha Buffelskloof Nature Reserve, are respectfully acknowledged. This nature reserve, which includes the largest tract of privately owned indigenous forest in Limpopo and Mpumalanga, is situated south of Mashishing



FIGURE 5.—Detail of *Xerophyta burrowsiorum*: a, flower opened to reveal attachment of stamens on tepals,  $\times 2$ ; b, external view of flower with glabrous pedicel and ovary,  $\times 2$ ; c, detail of leaf,  $\times 10$ ; d, style and stigma,  $\times 5$ ; e, stamen,  $\times 5$ ; f–h, variation in leaf shape,  $\times 2$ . Artist: Sandra M. Burrows.

(Lydenburg). It also housed the Buffelskloof Herbarium (BNRH) (now kept at J) that was conscientiously developed and augmented by the curatorship of John and Sandie; ultimately receiving international recognition.

*Xerophyta burrowsiorum* has been observed in flower during January and February, but like many of the xeric species of *Xerophyta* is likely to flower opportunistically or episodically in response to an adequate amount of rain. Thus, flowering can occur at any time, even after unseasonal rains in the middle of winter (Van Wyk & Hyde-Johnson 2021). Flowers remain open for about four days and are initially white but colour up through lilac to shades of pinkish mauve by the end of anthesis. We observed a small bee visiting some flowers (Figure 7), but no beetles in the flowers, as is common in members of the *X. retinervis* Baker group. Capsules mature soon after anthesis and nod from the tips of the pedicels. The base of the capsule ruptures to allow seed dispersal by wind or water.

Afrikaans common names for members of the genus include *besembos*, *bobbejaanstert* and *olifantstert* (Smith 1966). Currently no known common name exists for the new species.

The current known distribution of *Xerophyta burrowsiorum* is restricted to the Lisbon River Valley in Mpumalanga on the farms New York 530KT and Berlyn 506 KT (Figure 8). It is also likely to occur on Ponieskranz 543KT and Ledovine 507KT. Current collections range



FIGURE 6.—Putative hybrids between *Xerophyta burrowsiorum* and *X. sp. aff. X. viscosa*: a, growing on lip above cliff, note thick stems, black leaf sheaths and short broad leaves; b, pedicel and ovary with glands; c, pedicel and ovary of a plant in a different subpopulation, with finer glands. Photographs: K. Balkwill.

in altitude between 1 200 m and 1 350 m. This distribution is within the recently recognised Limpopo–Mpumalanga–Eswatini Escarpment Centre of Endemism (Clark et al. 2022) and this species is referred to as *Xerophyta* sp. B (Lisbon Falls), *Burrows 10620* (BNRH) in Appendix 2 of that publication.

The current known Extent of Occurrence (EOO) is 1 km<sup>2</sup>, but it is more likely to be in the region of at least 10 km<sup>2</sup>. Suitable habitat will be less than 10% of the EOO, so that the known Area of Occupancy (AOO) will be less than 10 ha and likely AOO may be 1 km<sup>2</sup>. Current estimates of the known subpopulations would total  $\pm$  3 000 individuals and so may be in the region of 30 000 in total. Some habitat has been lost to *Pinus patula* Schiede ex Schltdl. & Cham. plantations and there are escapes from these plantations threatening unplanted areas. Alien invasive species, including *Rubus* sp. and *Acacia mearnsii* De Wild., are also present. In addition, there is informal



FIGURE 7.—Flower of *Xerophyta burrowsiorum* with a potential pollinator caught by a spider. Photograph: S. Burns.

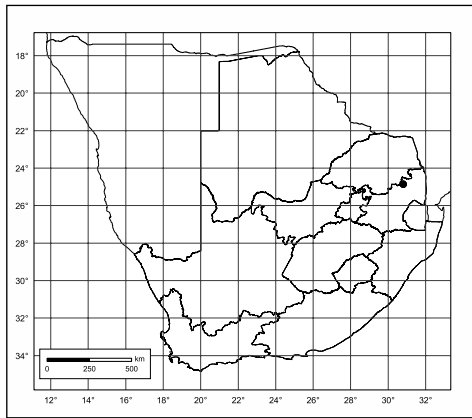


FIGURE 8.—Known geographical distribution of *Xerophyta burrowsiorum*.

gold mining taking place in the valley, adding another threat. None of the known localities is in a proclaimed nature reserve. The assumed historical loss of individuals due to afforestation is less than the thresholds for Criterion A (IUCN 2012). Although the EOO and AOO fulfil the criteria for Critically Endangered under Criterion B, and although there are currently less than 10 locations known (Criterion B2a), *Xerophyta burrowsiorum* does not fulfil Criteria B2b or B2c. Under Criterion C, *X. burrowsiorum* fulfils the criterion for Vulnerable for the number of mature individuals, but it does not fulfil the criteria for decline (i.e., Criterion C1 or C2). Under Criterion D, the number of individuals is more than 1 000 and although the AOO is much less than 20 km<sup>2</sup>, the threats

are not likely to raise the taxon to Critically Endangered or Extinct in a short time, thus *X. burrowsiorum* does not qualify. No quantitative analysis has been done to facilitate application of Criterion E. Thus, we propose a provisional threat status of Least Concern.

If *Xerophyta burrowsiorum* were to be introduced into general horticulture its potential may be limited to pot plant use and then perhaps only by specialist growers who may find the compact form of the plant most appealing. Furthermore, the general habit of intermittent/ sporadic flowering of most species of *Xerophyta* could limit its acceptance by gardeners. Most petaloid monocotyledons are relatively amenable to cultivation because of stored energy in their corms, bulbs or rhizomes and can even endure a prolonged seasonal period of storage in a dry paper packet. On the other hand, species of *Xerophyta* lack any such obvious survival strategy and have evolved a poikilochlorophyllous mode of existence instead. Two batches of seeds have been sown at Whyte Thorne Botanical Garden with successful results. A recent noteworthy account of *Xerophyta adendorffii* Behnke (Van Wyk & Hyde-Johnson 2021) provides greater detail on seed propagation for *Xerophyta* species in general.

### Additional specimens examined

SOUTH AFRICA, Mpumalanga: **2430** (Pilgrim's Rest): Lydenburg District, north of Graskop, west of Lisbon Falls, close to boundary between farms Lisbon 531KT, Berlyn 506KT and Ledovine 507KT (–DD), 10 February 2019, *McMurtry 17035* (HSMC,); Farm Berlyn 506KT, south of Berlin River (–DD), 3 February 2022, *McMurtry et al. 17500* (HSMC); *McMurtry et al. 17506* (HSMC); *McMurtry et al. 17507* (HSMC, J); *McMurtry et al. 17508* (HSMC, J); Lydenburg District, Graskop, below Lisbon Falls, Farm Ledovine 507KT, on boundary of Blyde Plantations, 1 260 m (north of Lisbon River) (–DD), 3 February 2022, *McMurtry et al. 17517* (HSMC, J).

**Description.**—Dwarf, perennial, poikilochlorophyllous, tufted herb. Stems short, hidden below leaves, radiating to form small, dense cushions, reaching 30(–50) mm long and 4–11 mm in diameter including persistent leaf bases, trichotomous; branches covered in fibres from dry, disintegrated leaf bases. Leaves persistent for an indeterminate period

( $\pm$  4–5 years), 3–5 arising from stem apex, tristichous, approximated, patent, slightly twisted in upper third; bases clasping,  $\pm$  10 mm long, initially white, outer surface of central blotch tan-brown, ageing brown; blades linear, narrowly lanceolate or narrowly oblong, shallowly M-shaped in cross-section, keel prominent  $(9\text{--}40\text{--}113) \times (2.0\text{--}3.8\text{--}6.5)$  mm; dull mid-green, depending on stage of desiccation or rehydration becoming yellow then maroon and finally light brown in dehydrated or resting stage, not viscid, both surfaces glabrous except for single row of minute strigose hairs along vein midway between midrib and margin, with three rows of minute pustules between midrib and row of strigose hairs and one row of the same pustules between the strigose hairs and margin, abaxially shallowly longitudinally grooved between veins, midrib grooved above, prominent below, conduplicate when dehydrated; margins and keel distinctly serrulate, teeth pointing towards leaf apex; tip broadly acute to acuminate, apiculate to aristate, apiculus straight, often dried brown; margin hyaline, whitish green. *Inflorescence* single on each stem, single flower from apical leaf axil; basal pedicel bracts in threes, to 15 mm long, green ageing brown, papyraceous; pedicel  $(58.0\text{--}62.1\text{--}86.0)$  mm long,  $\pm$  1 mm in diameter, round in cross-section, pale green flushed purple distally, without glands. *Flowers* bisexual, regular, 18–25 mm in diameter when open, narrowly to broadly campanulate. *Tepals* curving outwards apically, 3 + 3, nearly homochlamydeous, petaloid, free, narrowly elliptic, three outer  $20 \times 3.8$  mm, three inner  $18 \times 4.0\text{--}4.5$  mm, white, flushed light lilac, ageing to mauve; eglandular, apices acute. *Stamens* 3 + 3, attached to base of adaxial tepal surface; filaments 1.0–1.5 mm long, complanate, white; anthers basifixed, erect, 2.0–2.5 mm long, opening by longitudinal slits; outer series introrse; inner series latrorse; pollen grains shed as monads, yellow. *Ovary* inferior, doliform, 3-locular,  $2\text{--}3 \times 1.0\text{--}1.5$  mm, glabrous; ovule placentation axile on intrusive placentas, many per locule. *Style*  $\pm$  4.2–6.0 mm long,  $\pm$  1 mm in diameter, stigma columnar, triquetrous, tapering towards apex, longitudinally 3-grooved (stigmatoid bands), grooves of unequal length, 3.0–4.2 mm long,  $\pm$  1 mm in diameter. *Fruit* a capsule, nutant when ripe, borne on a bent scape, crowned with dried remains of the perianth, basally loculicidal, dehiscent. *Seeds* numerous, claviform,  $\pm$  1.2–1.5  $\times$  0.4 mm, honey-coloured. Plate 2383.

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*Watsonia humilis*

Iridaceae: Crocoideae

South Africa

**Watsonia humilis** Mill. in The Gardener's Dictionary 8: 2 (1768). *Gladiolus marmoratus* Lam.: 727 (1788). *Gladiolus roseoalbus* Jacq.: 7 (1797). *Watsonia roseoalba* (Jacq.) Ker Gawl.: t. 537 (1801). *Watsonia meriana* var. *roseoalba* (Jacq.) Baker: 158 (1877). *Watsonia litura* Klatt: 353 (1882). *Watsonia maculata* Klatt 352 (1882).

The genus *Watsonia* Mill. includes 53 species of deciduous or sometimes evergreen geophytes endemic to southern Africa, with its centre of diversity in the Cape Floristic Region in the southwestern part of the Western Cape Province, South Africa (Goldblatt & Manning 2020). A chorological analysis of distribution data of species in this genus also indicates additional centres of diversity (and probably endemism) along the eastern escarpment and seaboard of South Africa, as illustrated in the chorological map in Figure 1. *Watsonia humilis* is distributed within a particularly high area of diversity corresponding to the Hottentots-Holland area, as indicated in Figures 1 and 2.

The relationships of the genus lie with the other genera of subfamily Crocoideae with similar, deeply forked style branches and axillary corm development, together comprising the tribe Watsonieae Klatt (Goldblatt & Manning 2008). Molecular phylogenetic analyses retrieve *Watsonia* as sister to the monotypic *Pillansia* L.Bolus from the coastal mountains south of Caledon in the Western Cape Province, in a clade that also includes the small genera *Micranthus* (Pers.) Eckl. and *Thereianthus* G.J.Lewis (Goldblatt et al. 2006; Goldblatt & Manning 2020). Despite an apparently close relationship with *Watsonia*, *Pillansia* is morphologically unlike the former in both its solitary, strap-like foliage leaf lacking a midrib and its panicle inflorescence of actinomorphic flowers. The basic chromosome number for Watsonieae is evidently  $x = 10$  and *Watsonia* appears to be derived in its secondary base of  $x = 9$  (Goldblatt & Manning 2008).

Species of *Watsonia* have been recorded as edible and remnants of the corms of these plants have been found at the Klasies River archaeological site, dating back to the Middle Stone Age (Larbey et al. 2019). Even today, descendants of the Khoe-San still forage for these species' underground corms (Botha et al. 2020). Baboons, mole rats and porcupines also use the corms of watsonias as a food source (Duncan 2002) and dune rats are an apparent problem to several lowland *Watsonia* species as they seek out the corms as a food source (Waher 1974). In addition, it has been suggested that the gummy exudate from damaged corms of *Watsonia tabularis*, and possibly a diverse range of other *Watsonia* species, was used by early humans as a glue to cement stone heads (silcrete flakes) to spear and arrow shafts (Singels & Scoville 2018).

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PLATE 2384.—1, inflorescences with fully open and immature flowers,  $\times 1$ ; 2, globose corm with leaves,  $\times 1$ . Specimen depicted here was from cultivated material at Kirstenbosch, collected by Jane Forrester in the Somerset West area in 1998 (Kirstenbosch accession number 458/00). Voucher specimen: Forrester 1212 in National Herbarium (PRE), Pretoria. Artist: Gillian Condy.



PLATE 2384 *Watsonia humilis*



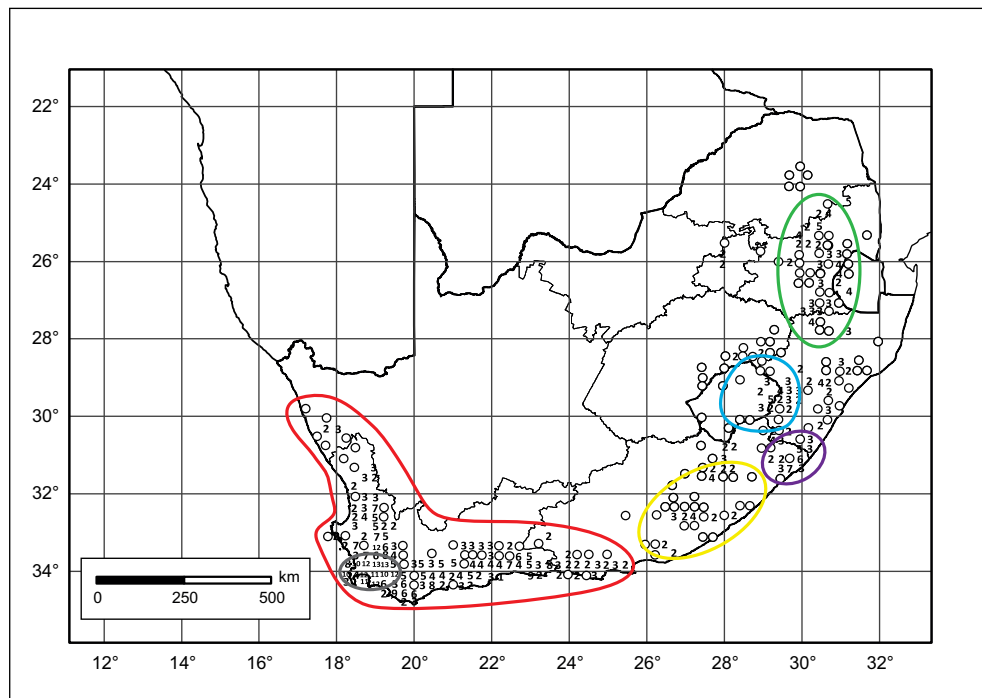


FIGURE 1.—Chorology of the genus *Watsonia*. Open circles indicate a quarter degree square (QDS) with a single species; all other numbers indicate number of species in each QDS. Centres of diversity are indicated by coloured shapes: red = Fynbos Centre with dark grey ellipse indicating the Peninsula and Hottentots-Holland area (where *Watsonia humilis* is found) as particularly high in diversity; yellow = Albany Centre; purple = Pondoland Centre; turquoise = Drakensberg Centre; green = Mpumalanga Escarpment Centre. Based on data obtained from SANBI NEWPOSA database.

*Watsonia humilis* was named by Philip Miller (1691–1771), an English botanist from Chelsea (Mills 2010), in the 8th edition of *The Gardeners Dictionary* (Miller 1768). The generic name honours Sir William Watson (1715–1787) and the species epithet, *humilis*, alludes to the short stature of the plant, among the shortest in the genus. The species is based on an illustration of a cultivated plant of unknown provenance that Miller published several years previously under the polynomial *W. humilis foliis linearis-ensiformibus* etc. The identity of Miller's plant was not immediately evident until it was linked by Goldblatt (1989) to the species that had until then been more commonly known under the later name, *W. roseoalba* (Jacq.) Ker Gawl. Until then, the name *W. humilis* was applied to purple-flowered plants from the Cape Peninsula that are now included in the more common *W. coccinea* (Herb. ex Baker) Baker (Goldblatt 1989) and the two species are still often confused. Both are dwarf species, but the flowers of *W. coccinea* have significantly longer filaments (25–30 mm long) that are well exserted from the perianth tube, whereas *W. humilis* has distinctly shorter filaments (10–20 mm long) that are included or only shortly exserted (Goldblatt & Manning 2020). In addition, *W. humilis* has wider leaves than *W. coccinea* (8–14 mm versus 2–8 mm wide) and distinctive apically recurved bracts (Goldblatt & Manning 2020). The ranges of the two species overlap significantly but *W. humilis* is absent from the Cape Peninsula.

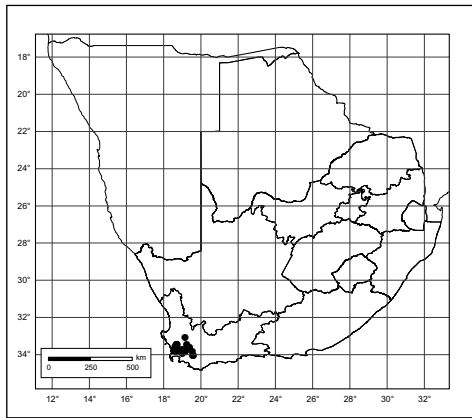


FIGURE 2.—Known geographical distribution of *Watsonia humilis* based on herbarium records.

*Watsonia humilis* has a narrow distribution in the Fynbos Biome in the Western Cape Province of South Africa, with historical records from Malmesbury to Gordon's Bay and inland to Worcester where it is mainly found in wet sandy soil on slopes and flats (Figure 2) (Goldblatt 1989; Goldblatt & Manning 2020). However, by 2013 only a single population remained in the wild (Goldblatt et al. 2013). Unfortunately, one additional population near Strand was destroyed by developers and the plants were relocated to a protected area by the City of Cape Town's Biodiversity Management Branch (R. Koopman, personal communication). With the advent of citizen science initiatives in South Africa (Hulbert 2016), such as iNaturalist (similar to the now discontinued iSpot), at least three

extant populations are now known (as shown in Figure 3). *Watsonia humilis* is thus considered to be Critically Endangered due to its small habitat range, as well as low numbers of reproducing individuals, which are under threat by habitat decline due to urbanisation and farming (Raimondo et al. 2009).

*Watsonia humilis* is one of the smaller watsonias, reaching up to about 300 mm in height, and therefore an ideal candidate for small gardens and pots. As in many geophytes, resprouting of *Watsonia humilis* corms is temperature sensitive. Exposure of the corms to higher temperatures for a short time delayed sprouting and prolonged exposure to temperatures above 20°C for a month resulted in 100% mortality. In contrast, resprouting was delayed by lowering the temperature below 10°C. Optimal temperature for seed germination was found to be 15–18°C (Waher 1974). While little is known about the cultivation of *W. humilis*, the successful cultivation of a co-distributed species, *W. strictiflora* Ker Gawl. can be achieved using a well-drained, slightly acid sandy media, made up of equal parts of coarse silica sand and finely sifted compost (Duncan 2015). The corm and later leafy shoots should be well watered twice a week throughout the winter months, with water withheld after flowering throughout summer. Little is known about pollination in *W. humilis*, but most of the pink-flowered species are pollinated either by bees (flowers with short perianth tubes) or long-proboscid flies (flowers with long perianth tubes) (Goldblatt & Manning 2020).

**Description.**—Deciduous geophyte, 100–400 mm high. *Rootstock* a globose corm, 10–20 mm in diameter, rooting from below, outer tunics finely netted, brown. *Stem* aerial, simple or with an occasional short branch. *Leaves* 5 or 6, mostly basal, lanceolate, 8–14 mm wide, mostly half the height of the stem; cauline leaves smaller, clasping. *Inflorescence* a 6- to 12-flowered spike, bracts firm, green or reddish above, recurved apically, (15–)20–30 mm long, inner  $\pm$  two-thirds as long, forked apically. *Flowers* zygomorphic, white tinged pink with pink tube, or pale to deep pink; perianth tube with lower part



FIGURE 3.—*Watsonia humilis* in habitat: a, whole plant in situ; b, single inflorescence; c, multiple inflorescences; d, close-up image of flower with beetle visitors. Photographs: a, R. Koopman; b–d, T. Rebelo.

(13–)17–30 mm long, upper part subcylindric, (13–)17–30 mm long,  $\pm 5$  mm in diameter at mouth; tepals oblanceolate to obovate, 15–22  $\times$  7–12 mm. *Stamens* arcuate, filaments (10–)15–20 mm long, not or barely exerted up to  $\pm 5$  mm; anthers 5–7 mm long, dark blue or violet. *Style* dividing between middle and apex of anthers, style branches 2–4 mm long. *Capsules* oblong, 15–20 mm long. *Seeds* 8–12  $\times$   $\pm 3$  mm, light brown,

2-winged with distal wing largest or proximal wing vestigial. *Flowering time*: late September to early November. *Chromosome number*:  $n = 9$ . Plate 2384.

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*Protea caffra* subsp. *caffra*

Proteaceae: Proteioideae

*Eswatini, Lesotho, Mozambique, South Africa*

**Protea caffra** Meisn. in A. de Candolle, *Prodromus systematis naturalis regni vegetabilis* 14: 237 (1856); Hutchinson et al.: 585 (1912); Beard: 49 (1958); Rourke: 50, t. 1 (1980); Rebelo: 32, t. 2 (2001); Van Wyk et al.: 247 (2000). *Scolymocephalus caffer* (Meisn.) Kuntze: 581 (1891). *Protea rhodantha* Hook.f.: t. 7331 (1893). *Protea baurii* E.Phillips: 230 (1910). *Protea bolusii* E.Phillips: 231 (1910). *Protea multibracteata* E.Phillips: 230 (1910). *Protea natalensis* E.Phillips: 231 (1910). *Protea peglerae* E.Phillips: 230 (1910). *Protea stipitata* E.Phillips: 104 (1934).

The commonest and most widespread *Protea* in South Africa is *Protea caffra*, which is acknowledged in its English and Afrikaans common names, namely common sugarbush and *gewone suikerbos* respectively (Rourke 1980; Rebelo 2001). *Protea caffra* is also at times referred to as the Highveld sugarbush, which is a misleading name because it occurs from near sea level to elevations of over 2 000 m in South Africa (Rourke 1980; Rebelo 2001). Common protea is also sometimes used, but the International Protea Association allows any member of the Proteaceae to be called ‘protea’ while ‘sugarbush’ is the recommended English common name for *Protea* species (Rebelo 2001).

Sugarbushes are characteristic and charismatic members of the Fynbos Biome and Cape Floral Kingdom (Mucina & Rutherford 2006), and most are Cape endemics (Rourke 1980). *Protea caffra*, however, is not found in the Western Cape and is instead a member of a clade of non-Cape species that diversified from a single ancestor that arrived from the Cape (Valente et al. 2010). Common sugarbushes are variable and six subspecies are recognised (GBIF Secretariat 2021). Two subspecies occur in South Africa, namely *P. caffra* subsp. *caffra*, which is the subject of this account, and the sickle-leaved sugarbush *P. caffra* subsp. *falcata* (Beard) Lötter. The sickle-leaved sugarbush has narrower and more sickle-shaped leaves than the common sugarbush and is confined to the Barberton Centre of Endemism in Mpumalanga Province, South Africa and Eswatini (Schmidt et al. 2002). *Protea caffra* subsp. *caffra* occurs from the Katberg of the Eastern Cape through KwaZulu-Natal, Lesotho, Eswatini, the Lubombo or Lebombo Mountains of southern Mozambique, to the northern provinces of South Africa (Figure 1). Beyond South Africa, the species is found as far north as Central and East Africa (GBIF Secretariat 2021). The specific epithet *caffra* is derived from Caffraria or Kaffraria, which is an old name for the eastern part of southern Africa, a name that was later more narrowly applied to a part of the Eastern Cape (Pooley 2003). *Protea* is named after Proteus, the Greek sea god who could change his appearance, an apparent allusion to the large variety of growth forms in the Proteaceae (Pooley 2003).

Summer-rainfall sugarbushes can be difficult to identify and *Protea caffra* subsp. *caffra* may be confused with several species where their ranges overlap. *Protea caffra* grows as a tree or multi-stemmed shrub (Figures 2 and 3) and is one of the grassland sugarbushes

PLATE 2385.—1, flowering branch,  $\times 0.5$ ; 2, single nutlet,  $\times 1$ . Voucher specimen: J.E. Burrows 15123 previously in Buffelskloof Nature Reserve (BNRH), Lydenburg, now in C.E. Moss Herbarium (J), Johannesburg. Artist: Gillian Condy.



PLATE 2385 *Protea caffra* subsp. *caffra*



in section *Leiocephalae* (Rebello 2001). The dwarf grassland sugarbush, *P. simplex* E.Phillips, is a close relative and for much of its range it may grow with *P. caffra* subsp. *caffra* (Rebello 2001). While the common sugarbush is often a small tree, *P. simplex* differs in being less than a metre high with multiple erect, slender, unbranched stems arising from a woody rootstock, and in having hairless involucre bracts (Rebello 2001). The Drakensberg sugarbush, *P. dracomontana* Beard, is also a rarely branched dwarf shrub and is confined to the Drakensberg escarpment of the Eastern Cape, KwaZulu-Natal, Free State and Lesotho, with a disjunct population in eastern Zimbabwe (Rebello 2001). It has broad, thick leaves and a woody rootstock and requires regular fires to maintain vigour (Beard 1958; Rourke 1980). *Protea gagedi* J.F.Gmel. is

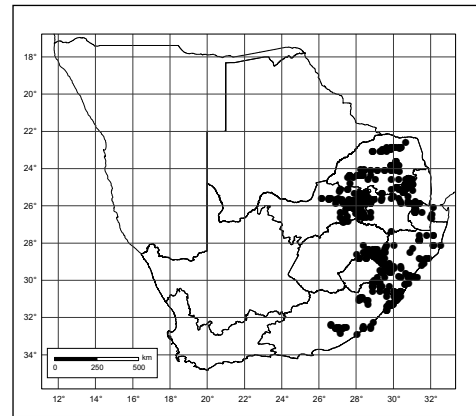


FIGURE 1.—Known distribution of *Protea caffra* subsp. *caffra* based on occurrence data from the Global Biodiversity Information Facility (GBIF 2022). The subspecies *falcata* occurs in Mpumalanga, South Africa, and northern Eswatini, and several other subspecies occur further north.



FIGURE 2.—Common sugarbush tree showing typical irregular crown at Injisuthi in the KwaZulu-Natal Drakensberg. Photograph: R.G.C. Boon.



FIGURE 3.—*Protea caffra* subsp. *caffra* growing as a multi-stemmed shrub at Krantzloof Nature Reserve, Durban, KwaZulu-Natal. Photograph: R.G.C. Boon.

in section *Lasiocephalae* and as such is one of the savanna sugarbushes (Rebello 2001). It can be separated from *P. caffra* subsp. *caffra* by its densely hairy young growth, depressed globose flower heads and the hairs on the outer involucral bracts are retained longer than in common sugarbushes (Rebello 2001; Schmidt et al. 2002). The flower heads in *P. caffra* open after the seeds are shed, whereas in *P. gagedi* the inflorescences remain cup-shaped (Coates Palgrave 2002).

*Protea caffra* subsp. *caffra* was first collected by Dr Christian Ferdinand Friedrich Krauss who arrived in Durban on 10 June 1839 aboard the *Mazeppa* with Swede Johan August Wahlberg and Frenchman Adulphe Delegorgue (Glen & Germishuizen 2010). His collection was made somewhere between Durban and Pietermaritzburg before he travelled back to Cape Town on 5 February 1840 (Rourke 1980; Glen & Germishuizen 2010). While Krauss's was the first gathering, the type specimen (Zey-

her 1458) was collected in about November or December 1841 in the Magaliesberg during Karl Zeyher and Joseph Burke's plant and animal hunting expedition to the interior of South Africa (Rourke 1980; Glen & Germishuizen 2010).

Common sugarbushes are found in sourveld grasslands and various bushveld or savanna types across a wide elevation range (Beard 1958; Rourke 1980). In hilly or mountainous country, *Protea caffra* is said to grow on south-facing slopes, but it is also found in areas of low relief (Rourke 1980). Research into changes in the distribution and abundance of common sugarbushes at five sites in the Central and Northern Drakensberg found plants growing on slopes of all aspects (Poultney 2014), which matches the author's (RGCB) own observations. *Protea caffra* favours poor, acidic, sandy or quartzitic soils, but will grow on a wide range of geological formations (Rourke 1980). In the KwaZulu-Natal Drakensberg it is found in the montane and sub-alpine belts associated with the Clarens Formation, previously known as Cave Sandstone (Hilliard & Burt 1987).

While exploring the coastal hinterland of KwaZulu-Natal, Krauss would have found common sugarbushes growing as scattered trees or in small colonies in grassland or open savanna. Had his first encounter with the plant been in the Drakensberg, he probably would have seen it growing in large, monospecific or perhaps mixed stands including *Protea simplex*, or the silver sugarbush, *P. roupelliae* Meisn. subsp. *roupelliae*. These sparse woodlands or 'protea savannas' (Figure 4) can cover large areas in high altitude grasslands (Hilliard & Burt 1987; Van Wyk et al. 2000; Mucina & Rutherford 2006).

The peak flowering season for common sugarbushes is late spring to midsummer, but flowering can occur at other times and is earliest at the coast and later in upland areas (Rourke 1980; Rebelo 2001; Calf & Downs 2002). Malachite Sunbirds and Gurney's Sugarbirds are conspicuous visitors to flowering common sugarbushes (Figure 5), silver sugarbushes and other proteas and plants that provide rich nectar in the Drakensberg and KwaZulu-Natal Midlands (Hilliard & Burtt 1987; Calf et al. 2001; Calf & Downs 2002). Gurney's Sugarbirds time their breeding to coincide with *Protea* flowering and nest mainly in sugarbush trees (Calf & Downs 2002). Many insects also visit *P. caffra* inflorescences (Figure 6) with fruit and flower chafers, scarab beetles in the sub-family Cetoniinae, acting as important pollinators (Steenhuisen & Johnson 2012b). The beetles have been shown to be effective agents of cross pollination and out-crossing rates were not reduced when birds



FIGURE 4.—*Protea caffra* subsp. *caffra* forming protea savanna in Gold Reef Mountain Bushveld at Rangeview near the Walter Sisulu National Botanical Garden, Gauteng. The original road between Johannesburg and Krugersdorp is visible in the background. Note the blue-green leaves, which is common in Highveld plants. Photograph: R.M. Gill.



FIGURE 5.—Gurney's Sugarbird on a common sugarbush inflorescence at Giants Castle camp in the KwaZulu-Natal Drakensberg. Photograph: C. Botha.



FIGURE 6.—Branch and single inflorescence at Krantzklouf Nature Reserve near Durban, KwaZulu-Natal. The rear end of a zigzag fruit chafer (*Anisorrhina flavomaculata*) is visible. Photograph: R.G.C. Boon.

were excluded from common sugarbush inflorescences (Steenhuisen et al. 2012). *Protea caffra* has colourful bracts (Figure 7) and produces nectar containing xylose, which are features of bird-pollinated proteas (Steenhuisen & Johnson 2012b). The species also demonstrates floral traits indicating that it has adapted to beetle pollination. These include open, bowl-shaped inflorescences (Figure 7), a strong fruity scent, and abundant and accessible pollen and nectar (Steenhuisen et al. 2010; Steenhuisen & Johnson 2012a). In *P. caffra* the scent is papaya-like, changing to the odour of fermenting fruit as the inflorescences age (Steenhuisen et al. 2010). Besides relying on insect and bird pollination, *P. caffra* subsp. *caffra* and other members of the clade of summer-rainfall grassland sugarbushes have been shown to be self-compatible and facultatively autogamous (Steenhuisen & Johnson 2012a). Fruits are released 9–12 months after flowering (Figure 8) and are wind-dispersed (Rebello 2001).



FIGURE 7.—Flowering plant at Injisuthi in the KwaZulu-Natal Drakensberg. Photograph: R.G.C. Boon.

While the subspecies is not considered to be threatened and has been assessed as Least Concern in the South African Red List of Plants, some populations are harvested for firewood or were cleared for forestry plantations in the past (Van Wyk et al. 2000; Pooley 2003; Mtshali et al. 2019). Fire is a regular feature of South African grasslands and savannas and a potential threat to woody plants growing in these vegetation types. With their thick bark (Figure 9) and their ability to recover from sub-cortical buds, mature common sugarbushes are well-suited to withstand fires if they are not too intense (Rourke 1980; Hilliard & Burt 1987). Seedlings develop subterranean lignotubers in their first year and, although many young plants are killed by fire, in normal circumstances some always survive (Rourke 1980). Fire regimes are important and too frequent fires may prevent recruitment and maturation (Bond 2008;



FIGURE 8.—Mature infructescence with hairy nutlets near Impendle in the KwaZulu-Natal Midlands. Photograph: S.L. Louw.

Kheswa et al. 2020), and high intensity fires, as occurs for example in bracken (*Pteridium aquilinum* (L.) Kuhn) patches, kill more *Protea caffra* trees of all size classes and suppresses regeneration (Adie et al. 2011). Repeat photographs taken in 2014 have shown that in some areas of the KwaZulu-Natal Drakensberg common protea numbers have increased since 1950–1995 (when the original photographs were taken), which may be in part due to increasing atmospheric CO<sub>2</sub> concentrations (Poultney 2014). If left undisturbed, trees are estimated to live for 100 years (Rourke 1980).

*Protea caffra* is the recorded host plant of two butterfly species, namely the range-restricted iNkomasi Protea (*Capys penningtoni*, also commonly known as Pennington's Protea) (Figure 10) and the more widespread Russet Protea *Capys disjunctus* (Woodhall 2020). The iNkomasi Protea is Critically Endangered and confined to



FIGURE 9.—Thick bark protects common sugar-bushes from most fires. Photograph: R.G.C. Boon.



FIGURE 10.—Critically Endangered iNkomasi Protea butterfly: a, male underside; b, male upperside. Photographs: S.E. Woodhall.

protea savanna in the KwaZulu-Natal Midlands and Drakensberg foothills (Armstrong 2020; Kheswa et al. 2020). The two major threats impacting the survival of the butterfly are the introduced harlequin ladybird beetle (*Harmonia axyridis*) that may predate on the butterflies' eggs and larvae, and hotter and more frequent fires that kill common sugarbushes (Armstrong 2020; Khewsa et al. 2020).



FIGURE 11.—Inflorescence shortly before anthesis at Rangeview near the Water Sisulu National Botanical Garden, Gauteng. This specimen has dense, silver hairs on the perianth limbs and margins of the involucral bracts. Photograph: R.M. Gill.

Zulu names for the common sugarbush are *uhlikihlane* and *isigalaba* (Pooley 2003). Doke & Vilakazi (1958) give *isigalaba sentaba*, which means 'protea of the mountain' and applies to *Protea caffra* and *P. roupelliae*. Bark from stems and roots is used to treat bleeding stomach ulcers and diarrhoea (Van Wyk et al. 1997). In Xhosa the name *isiqwane* is used for sugarbushes in general and *isadlunge* for the larger species (Peter et al. 2017). In Pondoland *isigalaba* is used to heal broken bones and treat a condition in babies known as *iqabaza* where hair turns reddish brown and stools are bloody (Zukulu et al. 2012). Seeds are used by the Bapedi to treat chlamydia (Semenya et al. 2013). Van Wyk et al. (2000) record that fruit and bark are used for dizziness and the bases of flower heads are used for treating psychological disorders. Numerous common names have also been recorded in Swati, Venda and Southern and Northern Sotho.



FIGURE 12.—Lateral view of an inflorescence shortly before anthesis near Impendle in the KwaZulu-Natal Midlands. Note the glabrescent involucral bracts, the tawny indumentum on the flowers and the green leaves typical of KwaZulu-Natal plants. Photograph: S.L. Louw.

Rourke (1980) opined that *Protea caffra* has little to offer as a garden subject other than that it can withstand cold and dry winters, although young plants should be protected from frost (Vogts 1989). However, *Protea caffra* has been successfully used in the excellent landscaping at Ezemvelo KZN Wildlife's Giants Castle rest camp. With the growing interest in indigenous gardening and landscaping, and fewer locally indigenous *Protea* species to choose from, many summer-rainfall gardeners would probably be pleased to have common sugarbushes in their collections. Plants may be raised from seeds sown in summer and will flower (Figures 11 and 12) in about five years (Rourke 1980; Pooley 2003). Cultivation is difficult, unless care is taken to avoid soil disturbance that damages the delicate proteoid roots (Vogts 1989). *Protea caffra* will prefer a sunny position and soils that are well drained, low in nutrients and acidic (Vogts 1989). At five years, trees will be about a metre tall and lower branches can be pruned to shape them (Rourke 1980).

**Description** (after Beard 1958; Rourke 1980; Rebelo 2001).—Erect, evergreen, single-stemmed tree, branching low down, up to 8 m tall, or a multi-stemmed, branched shrub up to 3 m tall, with a lignotuber especially in young and frequently burnt specimens. *Trunk* up to 400 mm in diameter. *Bark* thick, rough, deeply cracked into irregular blocks when mature, black, brown or grey. *Crown* irregular, rounded to spreading. *Branchlets* up to 12 mm in diameter, pinkish green, glabrous. *Stipules* absent. *Leaves* simple, alternate, spirally arranged, mostly clustered on recent growth, narrowly to broadly elliptic, oblong, oblanceolate (or falcate), 70–170 × 13–30 mm, base tapering, apex acute to obtuse, margin entire, glabrous, coriaceous when mature, pale green or bluish green, midrib pale, often pink towards the base, new growth reddish. *Petiole* absent or very short. *Inflorescence*

terminal, usually solitary or in groups of 3 or 4, globose to ovoid, broadly and shallowly crateriform when open, 40–70 mm in diameter, sessile or stalk up to 25 mm long, glabrous to densely sericeous. *Receptacle* hard, woody, broadly convex to flat, 20–30 mm in diameter. *Involucral bracts* 6–8-seriate, usually green and cream towards the base with various shades of pink to pinkish red towards the apex; outer series ovate to deltate,  $5\text{--}7 \times 10\text{--}20$  mm, tightly overlapping, glabrous or sparsely to densely sericeous distally, indumentum silvery or rust-brown, lost soon after flowering; inner series oblong to broadly oblong-spathulate,  $30\text{--}50 \times 10\text{--}20$  mm, apices rounded to subacute, glabrous or sparsely sericeous in basal region. *Perianth* tepals 4, straight, 45–60 mm long, usually glabrous externally except at limb apices; tube winged, 10–14 mm long, inner surface glabrous to densely pubescent distally, indumentum tawny to whitish; claws filiform, inner surface often pubescent, glabrescent externally; limbs linear-elliptic, up to 15 mm long, villous on the abaxial limbs, indumentum tawny to whitish, apices reflexed to form short, acute horns. *Style* 40–60 mm long, curved inwards. *Pollen presenter* 7–12 mm long, linear-filiform, bent at junction with style. *Anthers* 4, subsessile, up to 10 mm long. *Ovary* 5–8 mm long, obconic, covered with long, straight tawny hairs. *Hypogynous scales* acute, 2 mm long. *Fruit* a nutlet covered in long, red-brown hairs. Plate 2385.

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PLATE 2386 *Kalanchoe daigremontiana*

*Kalanchoe daigremontiana*

Crassulaceae: Kalanchooideae

Madagascar

***Kalanchoe daigremontiana*** Raym.-Hamet & H.Perrier in *Annales du Musée Colonial de Marseille*, sér. 3,2: 128 (1914); Boiteau & Mannoni: 44–46, three unnumbered figures (1949); Raymond-Hamet & Marnier-Lapostolle: 44, Plate XIII, Figures 35–37, Plate XIV, Figure 38 (1964); Jacobsen: 284, Plate 103, Figure 3 (left) (1977); Maire: 266 (1977); Jacobsen: 612, Figure 852 (1986); Boiteau & Allorge-Boiteau: unnumbered plate on unnumbered page facing p. 92, 94 (1995); Rauh: 116–117, Figure 287 (1995); Rauh: 130, 317–319, Figures 1183 & 1187 and, likely, 1188 (1998) [however, although labelled as ‘*K. daigremontiana*’, Figures 1184–1186 and, likely, 1189 in Rauh: 318–319 (1998), are referable to *K. laetivirens* Desc., which was treated as *K. ×laetivirens* by Smith: 105 (2020a)]; Sajeva & Costanzo: 172, centre left (2000); Descoings: 153 (2003); Smith et al.: 250 (2019); Smith & Shtein: 244 (2021). *Bryophyllum daigremontianum* (Raym.-Hamet & H.Perrier) A.Berger: 412 (1930). Lauzac-Marchal: 2508 (1974); Walters et al.: 249 (2011).

The first Malagasy species of *Kalanchoe* Adans. (Crassulaceae subfam. Kalanchooideae A.Berger emend. Gideon F.Sm. (see Smith & Monro (2022a, b) for the nomenclature to be used for this subfamily) to have been figured in the pages of *Flowering Plants of Africa* (FPA) was, perhaps appropriately, *K. tubiflora* (Harv.) Raym.-Hamet, treated there as *Bryophyllum delagoense* (Eckl. & Zeyh.) Schinz (however, see Figueiredo & Smith (2017) for the nomenclature to be used for this species). Given its ability to rapidly spread and colonise new habitats and niches through the remarkably effective dispersal and eventual establishment of vegetative propagules, this species is well-known globally – for the wrong reasons – especially in mild-climate parts of the world. This has given rise to *K. tubiflora* being known in the vernacular in English as mother-of-millions and as pregnant plant, these names being a clear reference to the large number of plantlets it produces on its leaves. In the text that accompanied botanical artist Gillian Condy’s plate of *K. tubiflora* in FPA, Tölken & Leistner (1986: second unnumbered text page after Plate 1938) noted that: ‘Our plant [...], *B. tubiflorum*] reproduces with such ease and speed, both vegetatively and by seed, that it is often considered a weed. Yet it is undoubtedly showy and attractive, and there can be little doubt that it would be a collectors’ item if it was rare and difficult to grow.’

This statement very much also applies to *Kalanchoe daigremontiana* Raym.-Hamet & H.Perrier, the subject of the present contribution, for if it was not for its ability to produce large numbers of bulbils on its leaf margins during its vegetative phase (Figure 1) and, post-flowering, on its single, but branched inflorescence (Figure 2), it would likely have been an exceedingly popular and treasured garden subject. Unfortunately, as in the case of *K. tubiflora*, the propagules of *K. daigremontiana* easily strike root and will densely populate virtually any substrate suitable for root development around the mother plant and well beyond. This results in unwanted material often being disposed of inappropriately, which in turn has contributed to the species having spread, usually uncontrollably, in places well away from its rather limited natural distribution range in central-southwestern Madagascar (Boiteau



FIGURE 1.—*Kalanchoe daigremontiana* is constitutively phyllo-bulbiliferous with a large number of plantlets invariably developing on short, guttered, downward-pointing pedestals along the irregularly crenate leaf margins during, especially, the juvenile (vegetative) phase of growth. Photograph: G.F. Smith.



FIGURE 2.—As a further reproductive strategy, large, fairly sparsely arranged bulbils are carried on the inflorescence of *Kalanchoe daigremontiana* after the flowers have wilted. Photograph: G.F. Smith.

& Allorge-Boiteau 1995 [Map 8]; Allorge-Boiteau 1996; Cristini 2020 [Maps 1 and 2]) (Figure 3). Today the species has been recorded from countries such as China, Mexico, the USA, Bahamas, Cuba, Ecuador, Haiti, Dominican Republic, Puerto Rico, Venezuela, Italy, the Madeira archipelago (Portugal), the Canary Islands and Balearic archipelago (Spain), Australia, New Caledonia and New Zealand. For good reason, Swingle (1934) referred to this species as ‘the easiest plant in the world to propagate’. Interestingly though, in their Table [8.7] of vascular aquatic species recorded in Madagascar, Manjato et al. (2022) treated *K. daigremontiana* as an emergent herb in subarid climatic zones and noted its conservation status as ‘Endangered’.

Not only does *Kalanchoe daigremontiana* propagate itself vegetatively; it additionally produces copious amounts of seed,

with the seed generally germinating easily. In addition, seedling development is rapid – more so than in numerous other species of *Kalanchoe*. Also, although plants will almost invariably die completely after flowering, in rare instances plants have been observed to sprout from near the base or, through plantlet development, higher up along the desiccating stem-peduncle continuum (Figure 4).

*Kalanchoe daigremontiana* is a so-called constitutively phyllo-bulbiliferous species with, during a substantial part of its life cycle, bulbils invariably developing on short, down-curved pedestals that are borne along the indented leaf margins (see Smith et al. 2021a; Smith & Shtein 2021). Remarkably, even the bulbils will themselves produce bulbils (Figure 5). Appropriately, *K. daigremontiana* is therefore inter alia variously known in the vernacular as mother-of-thousands – not quite the ‘millions’ of *K. tubiflora* – and as maternity plant. Given its interesting and varied reproductive biology and the ease with which it can be cultivated, including in greenhouses associated with research facilities, this species has been investigated from several different perspectives on multiple occasions, with the results reported in the scientific and popular press. Aspects investigated include its systematics, cytogenetics, horticulture, invasions biology, (eco-)physiology, phenology and medicinal properties, among other thrusts (see Zeevaart 1958, 2009 (and references therein); as well as Herrera & Nassar 2009; Melnik 2010; Walters et al. 2011; Heras Gomis 2015; Bhatti 2018; Pérez 2018; Cuadros Gutiérrez et al. 2019; Smith et al. 2019; Smith & Shtein 2021; Baumstein 2022; Drumkeld 2022; Planta 2022; Tremblay 2022).

*Kalanchoe daigremontiana* hybridises easily with some other species of *Kalanchoe* (Resende 1956), including with *K. tubiflora*, with this hybrid in its own right having become a weed in some parts of the world (Silva et al. 2015; Smith et al. 2015) (Figures 6 and 7). The hybrid was described as *K. ×houghtonii* D.B.Ward and from it a number of cultivars,

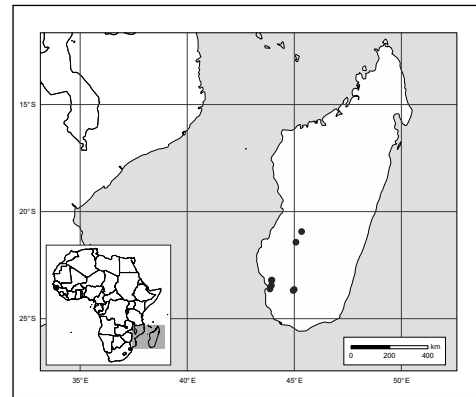


FIGURE 3.—Known natural geographical distribution range of *Kalanchoe daigremontiana* in Madagascar (see Boiteau & Allorge-Boiteau 1995 [Map 8]; Allorge-Boiteau 1996 [Map 9]; Cristini 2020 [Maps 1 and 2] and Shtein et al. 2021: 250). The species is widely naturalised in mild-climate parts of the world, possibly also in Madagascar, beyond its natural distribution range.

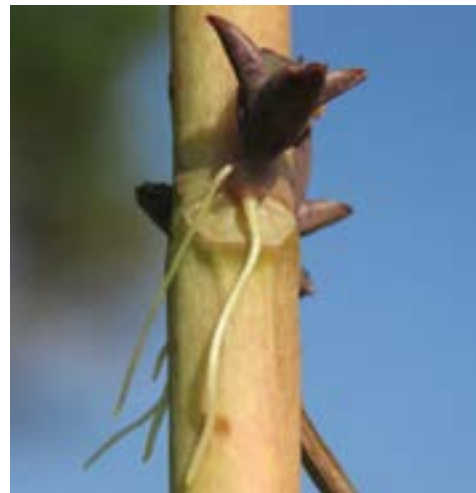


FIGURE 4.—Bulbils, some already forming roots, produced post-flowering on a peduncle of *Kalanchoe daigremontiana*. Photograph: G.F. Smith.



FIGURE 5.—Bulbils that developed on the leaf margins of *Kalanchoe daigremontiana* here developed their own bulbils. Photograph: G.F. Smith.

such as *K. ×houghtonii* ‘Garbí’, have been selected based on vegetative and/or reproductive characters (see for example Guillot Ortiz et al. 2014). Representatives of this hybrid are sometimes confused with *K. daigremontiana* (see for example Maire 1977: 266–267, Figure 95; Sajeva & Costanzo 2000: 172, top left; and Moore 2017: 254). Furthermore, in nurseries in the United Kingdom, *K. ×houghtonii* has largely replaced true *K. daigremontiana*, but such hybrid material is still and incorrectly sold under the name *K. daigremontiana*, as a narrow-leaved variant of the species (J.M.H. Shaw, personal communication, September 2022). While *K. ×houghtonii* has the general appearance and habit of *K. daigremontiana*, it tends to be a slightly smaller plant



FIGURE 6.—*Kalanchoe ×houghtonii* densely growing with a *Pelargonium* sp. (a geranium of the European horticultural trade) in a pot in the coastal town of São Brás de Alportel, in the district of Faro, in the Algarve in southern Portugal. Light green and white artificial flowers have been inserted into the centre of the pot. Photograph: G.F. Smith.



FIGURE 7.—*Kalanchoe x houghtonii* naturalised near Praia da Baía de Porto Covo, near Porto Covo, a coastal town in the district of Setúbal, Portugal. Also note the presence of the invasive South African weed *Oxalis pes-caprae* L. at this location. Photograph: G.F. Smith.

in all respects, and the leaves, while well-spotted with dark purplish brown blotches on a khaki-green background, in particular are usually shorter and narrower, and the basal ‘wings’ of the peltate leaf blades are generally much less pronounced, if present (Smith 2019). Leaves of *K. daigremontiana* are also light to mid- to dullish green and irregularly and, abaxially, variously spotted with purplish, dark pinkish, or brownish blotches (Figure 8). The leaves are elongated-triangular, irregularly folded lengthwise and at maturity often peltate with the basal blade ‘wings’ usually stretching well beyond the point of attachment of the petiole to the stem (Figure 9). These leaf characters have in turn given rise to the vernacular names devil’s backbone, Mexican hat plant and alligator plant. When in the juvenile, vegetative phase, and especially when under drought stress, the leaves of *K. daigremontiana* are short, closely packed and often variously down-curved to slightly distorted (Figure 10).



FIGURE 8.—The leaf blades of *Kalanchoe daigremontiana* are variously and irregularly purplish-, pinkish-, or brownish-mottled, especially abaxially. The mottling sharply contrasts against a light green to creamy-green background. Photograph: E. Figueiredo.



FIGURE 9.—At maturity the leaves of *Kalanchoe daigremontiana* are often peltate with the basal blade ‘wings’ usually stretching well beyond the point of attachment of the petiole to the stem. During the rainy season the internodes elongate substantially. When growing in shade, the leaves are much greener, especially adaxially. Photograph: G.F. Smith.

*Kalanchoe laetivirens* that was treated as *K. ×laetivirens* by Smith (2020a), which, like *K. daigremontiana*, can develop an extraordinary number of leaf- and, post-anthesis, inflorescence bulbils, has also been confused with *K. daigremontiana*, for example by Rauh (1998: 318–319, Figures 1184–1186 and, likely, 1189) and, more recently, by Moore (2017). However, *K. laetivirens* is often an overall lighter green entity that develops solitary, broad, densely foliated pseudo-rosettes, with the petioles generally being short and thick.

The pendent flowers of *Kalanchoe daigremontiana* vary from dull light to dark pinkish purple and are carried on a generally tall inflorescence that is apically branched and many-flowered. The peduncle remains straight and erect, and is a light greenish purple colour (Figure 11).

Along with *Kalanchoe tubiflora*, *K. daigremontiana* was included in the informal Groupe VI Bulbilliferae of Boiteau & Allorge-Boiteau (1995). More recently,

Shtein & Smith (2021) formally published the name *K. sect. Invasores* Shtein & Gideon F.Sm. for these two and related species, with the epithet ‘*Invasores*’ deliberately chosen as it means ‘invaders’ in Latin.

*Kalanchoe daigremontiana* is one of the few *Kalanchoe* species that is not burdened with a vast synonymy. Its only recorded synonym is *Bryophyllum daigremontianum*, which was published when Berger (1930) transferred the species to that genus, a classificatory view that we do not share in this work and that has not been followed in kalanchooid taxonomy for the past ca. 50 years. Hamet & Perrier de la Bâthie (1914), when publishing the name *K. daigremontiana*, noted that it was based on material that Joseph Marie Henri Alfred Perrier de la Bâthie (11 August 1873 [St.-Pierre-d’Albigny, near Chambéry, Savoie, France]–2/3 October 1958 [Chambéry, Savoie, France]) had collected in July 1910 in central-southwestern Madagascar (see Smith & Shtein 2021 for a detailed discussion). ‘Henri’ or ‘Henry’ Perrier de la Bâthie was an indefatigable collector of natural history specimens in Madagascar (Dorr 1997). For Perrier de la Bâthie the month of July 1910 was a productive period for the collecting of new kalanchoes in Madagascar, with several other species, such as *K. millotii* Raym.-Hamet & H.Perrier, also having been collected at this time (Hamet & Perrier de la Bâthie 1912; Shtein et al. 2021; Smith et al. 2021b).



FIGURE 10.—During the dry season the leaves of *Kalanchoe daigremontiana* are longitudinally folded upwards and often variously distorted. The leaves are closely packed especially during the vegetative, juvenile phase of plant development, as here. Photograph: G.F. Smith.

For three years, from 1912 to 1915, Perrier de la Bâthie, collaborated on the taxonomy of *Kalanchoe* with fellow Frenchman Raymond-Hamet (25 March 1890 [Dijon, Côte D’Or, France]–2 October 1972 [Paris, France]), who was then in his early-20s, and even at that age regarded as the global expert on *Kalanchoe* (Smith 2020b), particularly since he had produced a substantial, two-part monograph on the genus when still in his late-teens (Hamet 1907, 1908). Perrier de la Bâthie amassed a substantial herbarium of Malagasy material that was donated to the *Muséum national d’Histoire naturelle* in Paris, France, in the early 1930s. He had more than a passing interest in *Kalanchoe* and between 1923 and 1928 described, as sole author, 11 new species in the genus.

Raymond-Hamet, but not Perrier de la Bâthie, had a distinct preference to commemorate people in the specific epithets he chose for the new species of *Kalanchoe* he described, with *daigremontiana* being no exception. In the protologue of the name Raymond-Hamet and Perrier de la Bâthie stated: ‘Cette plante [*Kalanchoe daigremontiana*], qui est dédiée à Madame et Monsieur Daigremont ...’. Today very little is known about the Daigremonts, with Sánchez de Lorenzo-Cáceres (2015, 2016) only stating that the name: ‘... honra al Sr. y la Sra. Daigremont (fl. 1914), matrimonio francés estudiosos de las plantas alpinas y poseedores de una buena colección de crasuláceas en Soisy-sous-Montmorency’; English: ‘... honours Mr and Mrs Daigremont (who were active around 1914), a French married couple who studied Alpine plants and possessed a fine collection of Crassulaceae at Soisy-sous-Montmorency [north of Paris, France]’.

*Kalanchoe daigremontiana* is one of the easiest species of *Kalanchoe* to grow. Its multiple reproductive strategies make it very prolific in cultivation and plants very quickly



FIGURE 11.—The colour of the pendent flowers of *Kalanchoe daigremontiana* varies from dull light to dark pinkish purple. The inflorescence is apically branched and many-flowered. The peduncle remains straight and erect, and is a light greenish purple colour. Photograph: G.F. Smith.

become weedy in gardens and invasive in the wild. This species, therefore, should not be grown in mild-climate areas given its invasive tendencies. However, plants are often offered for sale in commercial nurseries (Figure 12). Plants are generally not cold-hardy and a heavy frost will kill them. As is the case with most species of *Kalanchoe*, the flowering of *K. daigremontiana* generally peaks in mid-winter.

**Description.**—Generally bi- or triennial, unbranched or rarely branched, glabrous, medium-sized, robust shrub-like succulent, to 0.8–1.4 m tall when in flower. *Stem* simple or rarely branched, erect or leaning and then curved upwards, green to yellowish or brownish. *Leaves* peltate with basal blade ‘wings’ stretching beyond point of petiole attachment for up to  $\pm 20$  mm, smooth, petiolate,  $\pm$  flattened above and below to strongly guttered, uniformly green or yellowish to brownish green adaxially, sometimes blotched brown to purple above point of petiole attachment, abaxially variously spotted with purplish, pinkish, or brownish blotches arranged into stripes

and skeleton-like configurations on light to creamy green background; petiole 10–40 mm long, green or yellow and purple-infused, generally not maculate, not amplexicaul, sub-cylindrical, succulent; blade 50–200  $\times$  20–60 mm, ovate to elongated-triangular, basally saddle-shaped, often irregularly folded lengthwise when under environmental stress, succulent; base broadened, rounded, usually peltate; apex acute-subacute; margins irregularly dentate with plantlets developing on ovate or spatulate pedestals of a few mm long, in notches between marginal dentations. *Inflorescence* a terminal, apically branched, many-flowered, head-shaped corymb or branched, seemingly compounded inflorescence consisting of 5–7(–10), successively produced corymbs arising from single peduncle, up to  $\pm 200$ –400(–700) mm tall, erect, often bulbiliferous after flowering, forming discrete, large bulbils, but not dense bulbil clusters; peduncle straight, light greenish to purple; pedicels 5–12 mm long, glabrous. *Flowers* pendent, glabrous, subtended by small bracts that soon shrivel, waxy bloom absent, papery when dry; *calyx* 4–5 mm wide, tubular for  $\pm$  half to two-thirds, succulent, shiny light green infused with purple to almost uniformly purple, purple more prominent towards calyx base and sepal tips and arranged in feint longitudinal lines; *sepals* 7–11 mm long, free portion short-lanceolate to elongated-triangular, fused for  $\pm 4$ –6 mm, 2.5–3.5 mm wide where fused, acute-tipped, obscuring  $\pm$  quarter of corolla tube; *corolla* pink-infused green around carpels, elsewhere dull light pinkish purple to dark pinkish purple, longitudinally infused with yellow in centre of petal; tube 15–19  $\times$  6–7 mm,  $\pm$  funnel-shaped, more or less cylindrical lower down, very slightly narrowed at carpel



FIGURE 12.—Bagged specimens of *Kalanchoe daigremontiana* (plants in the centre and back, on the left) offered for sale in the Djema el-Fna Square, Marrakesh, Morocco. Photograph: E. Figueiredo.

height, gradually widening higher up, flared at mouth; lobes  $7\text{--}10 \times 4\text{--}5$  mm, obovate, apically rounded-obtuse, minutely apiculate. *Stamens* inserted below middle of corolla tube at  $\pm$  upper level of carpels, included or hardly exerted; filaments  $12\text{--}15$  mm long, of two similar lengths, thin, bright purplish red; anthers  $\pm 1.0\text{--}1.5$  mm long, greyish black, rounded-cordate, hardly exerted. *Pistil* consisting of 4 carpels; carpels  $\pm 6\text{--}7$  mm long, shiny mid-green, attenuate towards styles; styles  $\pm 15$  mm long; stigmas very slightly capitate, green; scales  $\pm 1.5 \times 1.5$  mm, yellow-green,  $\pm$  square, slightly narrowing apically, free, slightly indented above. *Follicles*  $6\text{--}9$  mm long, light green, eventually brittle, grass spikelet-like when dry, enveloped in dry, dull purplish cream remains of calyx and corolla, calyx and styles persistent for a long time, dull purplish cream for a long time and remaining so. Seeds  $0.50\text{--}0.75$  mm long, small, light brown to reddish brown, rectangular-straight or banana-shaped-curved, slightly apiculate at one end, faintly longitudinally striated. *Chromosome numbers*:  $2n = 34$  (Baldwin 1938),  $2n = 34, 60, 68, 176$  (Sharma & Ghosh 1967; Smith 2022). (Note that the veracity of the identifications of the material of *Kalanchoe daigremontiana* studied by Sharma & Ghosh (1967) and for which they recorded  $2n$  numbers of 60 [a deviating number for *Kalanchoe*], 68 [tetraploid] and 176 [ $\pm$  decaploid] could not be verified and confirmed, and Smith (2022) interpreted the species as diploid.) Plate 2386.

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PLATE 2387 *Kalanchoe luciae*

*Kalanchoe luciae*

## Crassulaceae: Kalanchooideae

*Southern and south-tropical Africa (South Africa, Eswatini, Mozambique, Zimbabwe)*

***Kalanchoe luciae*** Raym.-Hamet in Bulletin de l'Herbier Boissier, ser. 2,8: 256 (1908b); Hamet: 21 (1910); Letty: 152 (1962); Raymond-Hamet & Marnier-Lapostolle: 91, Plate XXXIII, Figure 112–114 (1964); Ross: 179 (1972); Jacobsen: 287 (1977); Fernandes: 204 (1978); Jacobsen: 618 (1986); Smith et al.: 64–72, Figure 2, 5, 7 (2016); Smith et al.: 188–194 (2019a); Smith & Van Wyk: 169, 198, 199 (2019); Smith & Figueiredo: 213 (2021a). *Kalanchoe aleurodes* Stearn: 164 (1931a); Stearn: 464, Figure 239, 475 (1931b); Tutin: 9 (1931). *Kalanchoe albiflora* Forbes: 37 (1941). *Kalanchoe luciae* subsp. *luciae* Tölken: 89 (1978); Fernandes: 57 (1983); Tölken: 71, Figure 9,2 (1985); Retief & Herman: 392 (1997); Descouings: 164 (2003).

In 1907 and 1908, the teenaged French botanist, physician and lawyer, Raymond Hamet (1890–1972), who at the time still wrote his first name and surname without a hyphen – he eventually changed his name to Raymond-Hamet, i.e., by hyphenating his first and surname – authored a substantial two-part monograph of the genus *Kalanchoe* Adans. (Hamet 1907, 1908a; Smith 2020a). Shortly after the second part of Hamet's monograph appeared in print, he published the name *K. luciae* in the French journal *Bulletin de l'Herbier Boissier* (Hamet 1908b), which apparently was not widely available and in some circles the name went undetected for a long time, with synoptic treatments of the genus published subsequently only listing the name many years later (see for example Jacobsen 1977, 1986). The British botanist, William T. Stearn (1911–2011) was aware of the description of *K. luciae* but, based on the nectar scales of *K. luciae* being three-lobed, he described material collected in Zimbabwe as *K. aleurodes* Stearn, because the scales of his new species were found to be subentire ('sub-integræ') (Stearn 1931a, b). At present we retain the name *K. aleurodes* in the synonymy of *K. luciae* (see above), but note that a proposal to treat the name *K. aleurodes* as rejected under Article 56 of Turland et al. (2018) is under consideration, as Smith & Figueiredo (2021b) argue that it was the earliest description of the species today widely known as *K. wildii* Raym.-Hamet ex R.Fern.

In 1941, 10 years after the name *Kalanchoe aleurodes* was published, the lack of wide awareness of the earlier publication of the name *K. luciae* prompted Helena M.L. Forbes (1900–1959) (Figure 1), who had just been appointed as curator of the Natal Herbarium, now the KwaZulu-Natal Herbarium (Gunn & Codd 1981), to publish the name *K. albiflora* Forbes for material referable to *K. luciae* from eastern South Africa (Forbes 1941). The confusion around the name *K. luciae* persisted for many years and it was only by the 1970s that first Ross (1972), and soon thereafter Tölken (1978, 1985), started using the name *K. luciae*, which has priority. Today the name of the species is well-entrenched in the nomenclature of the genus and the identity of the species is no longer in question (Figure 2).

PLATE 2387.—1, basal pseudo-rosette of a plant that has initiated the development of an inflorescence,  $\times 0.66$ ; 2, middle section of an inflorescence,  $\times 1$ . Voucher specimen: G.F. Smith 1155 in H.G.W.J. Schweickerdt Herbarium (PRU), Pretoria. Artist: Gillian Condy.



FIGURE 1.—In 1941, Helena M.L. Forbes (1900–1959) published the name *Kalanchoe albiflora* for material referable to *K. luciae* from eastern South Africa. Photographer unknown. Copyright: South African National Biodiversity Institute. Reproduced with permission.



FIGURE 2.—The leaves of *Kalanchoe luciae* are often heavily purplish red-infused. In some instances its leaves, especially the outer ones, are virtually entirely red to reddish purple. This selection is often available in the horticultural trade under the moniker *K. luciae* ‘Red Lobster’. Photograph: G.F. Smith.

*Kalanchoe* is here regarded as consisting of five subgenera: the geographically widespread autonymic one; as well as *K. subg. Alatae* (Raym.-Hamet) Gideon F.Sm., Shtein & D.-P.Klein (Smith 2021a; Smith et al. 2021a), *K. subg. Bryophyllum* (Salisb.) Koord., and *K. subg. Kitchingia* (Baker) Gideon F.Sm. & Figueiredo (Smith & Figueiredo 2018a; Smith et al. 2021b), all three of which are endemic to Madagascar; and *K. subg. Fernandesiae* Gideon F.Sm. from southern and south-tropical Africa (Smith 2020b). It is especially *K. subg. Fernandesiae* that concerns us here.

An initial very wide interpretation of what constitutes *Kalanchoe thyrsiflora* Harv., which has vegetative and reproductive morphologies similar, but by no means identical, to that of *K. luciae*, also resulted in these two species being sometimes confused. Both sport medium-sized to large, paddle- to soup plate-shaped and -sized leaves (Figure 3). However, the leaves of *K. luciae* tend to be larger and more red-infused and the species has white to pale yellowish green corolla lobes (Figures 4 and 5), while those of *K. thyrsiflora* (Figure 6) are bright yellow. The natural geographical distribution ranges of *K. luciae* and *K. thyrsiflora* overlap to some extent and when not in flower the two species indeed can be easily confused. *Kalanchoe thyrsiflora* was the second *Kalanchoe* species to be described from South Africa (Harvey 1862) and the first to have been illustrated in [The] *Flowering Plants of [South] Africa* (Phillips 1929). Likely because of the confusion discussed above, *K. thyrsiflora*, but not *K. luciae*, has also featured in other works that emphasised botanical art, including those by Letty (1962) and Germishuizen & Fabian (1982, 1997).

Until recently two subspecies were recognised in *Kalanchoe luciae*: *K. luciae* subsp. *montana* (Compton) Toelken and the



FIGURE 3.—*Kalanchoe luciae* has round, soup plate-sized leaves carried in a pseudo-rosette borne atop a short, weak, eventually leaning to snake-like stem. Stems are to some extent strengthened by the conspicuous, rib-like leaf scars left where leaves abscised. Photograph: G.F. Smith.

autonymic one (Tölken 1978, 1985). However, *K. montana* Compton has been reinstated at species rank (Smith et al. 2016).

Material of two recently described species, *Kalanchoe winteri* Gideon F.Sm., N.R.Crouch & Mich.Walters (Crouch et al. 2016; Smith et al. 2019b) and *K. crouchii* Gideon F.Sm. & Figueiredo (Smith & Figueiredo 2018b; Smith et al. 2021c), that sport medium-sized to large, obovate to round leaves has also been, at least to some extent, confused with a very broadly circumscribed *K. luciae*. However, the leaves of *K. winteri* are basally auriculate and more widely dispersed along the stem than in *K. luciae*, and the corolla lobes of *K. winteri* are bright yellow, rather than white or pale yellowish green. *Kalanchoe crouchii*, on the



FIGURE 4.—The corolla lobes of the most wide-spread form of *Kalanchoe luciae* are bright white. The flowers are urceolate with the corolla lobes varying from erectly spreading to strongly recurved. Photograph: G.F. Smith.



FIGURE 5.—This form of *Kalanchoe luciae* has yellowish green corolla lobes. Corolla tubes of *K. luciae* are slightly four-angled and the corolla lobes are often strongly reflexed. Photograph: G.F. Smith.



FIGURE 6.—*Kalanchoe thyrsiflora* has bright yellow corolla lobes, unlike those of *K. luciae* that are white to pale yellowish green. Photograph: G.F. Smith.

other hand, is in all respects a daintier species and has yellow flowers that are similar to those of *K. thyrsiflora*.

What mostly contributed to the name *Kalanchoe luciae* being applied to a range of species today recognised as distinct are its overall vegetative morphology of soup plate-shaped and -sized leaves that are arranged basally in pseudo-rosettes, as well as its rather densely flowered, club-shaped inflorescences (Figure 7a). These morphologies have proven to be horticulturally very desirable and in places where there is sufficient space – for in time plants can grow quite big – *K. luciae* is very popular as a garden subject (Figure 7b).

Along with *Kalanchoe sexangularis* N.E.Br. (Tölken 1983; Figueiredo et al. 2016), *K. longiflora* Schltr. ex J.M.Wood (Smith & Figueiredo 2017) and *K. thyrsiflora*, *K. luciae* is the most commonly cultivated kalanchoe in southern Africa. Plants grow very easily and will flourish in virtually any type of soil. It will tolerate considerable neglect and still maintain its large, soup plate-sized and -shaped, pseudo-rosetately arranged leaves looking firm and healthy. The species is drought-hardy and requires minimum irrigation, looking none the worse for wear when subjected to aridity in summer and/or winter, even though its natural geographical distribution range is in a decidedly summer-rainfall region. When irrigation is limited or even entirely withheld for periods and plants are grown in full sun, the leaves of most forms take on a magnificent deep red to purplish red colour.

*Kalanchoe luciae* can be easily propagated from seed and seedlings develop rapidly. These can be transplanted to the places where they are intended to grow, usually within a single season. Alternatively, whole rosettes that arise from the base of a plant that has flowered can be removed



FIGURE 7.— *Kalanchoe luciae*: a, the inflorescences are densely flowered and cylindrical to club-shaped in outline; b, when allowed to branch from the base, plants of *Kalanchoe luciae* will in time develop into large clumps that consist of numerous pseudo-rosettes and, in the cold flowering months, several developing flowering stems. Photographs: G.F. Smith.

and planted where they are desired. *Kalanchoe luciae* flowers mostly in the autumn and winter months, from April to August, peaking from June to July (southern hemisphere), but plants that flower unseasonally are sometimes encountered. If temperatures drop below 0°C where they will be cultivated, it would be best to provide them with protection against frost (Figure 8).

Two cultivars selected from *Kalanchoe luciae* have recently become popular in gardening circles (Smith 2020c, d, 2021b). The first, *K. luciae* ‘Fantastic’, is a variegated-leaved form with the variegation becoming bright pink to purplish red when it is grown in full sun (Figure 9). Plants are slightly smaller- and slower-growing than regular *K. luciae*, likely as a result of less chlorophyll in the leaves, and have the appearance and general vegetative morphology of *K. thyrsiflora*. However, once plants flower there is no doubt that material belongs to *K. luciae* as the flowers are cigar-shaped rather than cylindrical and the corolla lobes are white, not yellow as in *K. thyrsiflora*.

A different leaf mutation is found in *Kalanchoe luciae* ‘Oricula’; material of this cultivar has narrowly oblong, marginally in-rolled leaves, and it is crested, a condition sometimes recorded in the family Crassulaceae (Figure 10).

*Kalanchoe luciae* was named for Mademoiselle Lucy Dufour (fl. 1908), a friend of Raymond-Hamet who described the species. The material on which the name was based was collected in 1904 at Spelonken in the Limpopo Province of South Africa by the missionary Henri Alexandre Junod (1863–1934) who, at the time, was stationed at Shiluvane in the then northeastern Transvaal, presently included in Limpopo (Gunn & Codd 1981; Ferreira 2013).

*Kalanchoe luciae* has a wide, essentially eastern, north-central, and northeastern natural geographical distribution range in mild-climate parts of South Africa (parts of North West, Gauteng, Limpopo, Mpumalanga and northern KwaZulu-Natal provinces, but it is absent from the climatically more severe Free State; (Retief & Meyer 2017)), Eswatini, Mozambique and Zimbabwe (Figure 11). The species usually occurs in grassy patches in savanna vegetation or often in exposed positions on rocky outcrops. Although its local distribution can be patchy, it is rather common in nature and not threatened; at least in South Africa its conservation status has been assessed as being Least Concern. In Zimbabwe it may be confused with the endemic *K. wildii* (Fernandes 1978, 1983).

The large, often perfectly round leaves of *Kalanchoe luciae* have given rise to the most widely used common names of the species: *sopbordplakkie* in Afrikaans and flipping flap-jacks or paddle plant in English.



FIGURE 8.—When temperatures drop below 0°C and remain at sub-zero levels for some days, plants of *Kalanchoe luciae* will succumb to frost damage (orange pink leaves). Photograph: G.F. Smith.

**Description.**—Perennial or short-lived multi-annual, few- to many-leaved, sparsely branched from near the base, glabrous, white-waxy, robust succulent, to 2 m tall. *Stem* arising from a slightly swollen rootstock, erect to leaning, then curved upwards, horizontally ridged where leaves abscised, greenish white. *Leaves* erect to patent erect, succulent, sessile,  $\pm$  flattened above, slightly convex below, light yellowish green to bluish green, infused with bright red especially apically and along margin; petiole absent; blade 40–160(–190)  $\times$  20–90(–110) mm, round to obovate to oblong, not folded lengthwise, sometimes wavy; base narrow; apex rounded-obtuse or slightly truncate; margins entire, often with substantial red tint. *Inflorescence* a club-shaped to cylindrical thyrses consisting of several dichasia terminating in monochasia, to 1.6 m tall, slender, erect to leaning, densely flowered; pedicels 4–6 mm long. *Flowers* erect to slanted horizontally, all parts except adaxial corolla lobe surfaces haphazardly covered with a thin to mostly substantial white waxy bloom; calyx light



FIGURE 9.—The leaves of *Kalanchoe luciae* 'Fantastic' are creamy- to white-variegated and turn bright pink to purplish red under conditions of high solar radiation. Photograph: G.F. Smith.

greenish white; sepals 3–6 mm long, short-triangular, almost free to the base, acute; corolla 8–13 mm long, much enlarged lower down, tapering to mouth, not twisted apically after anthesis; tube 7–12 mm long, light yellowish green, more or less quadrangular-urceolate, enlarged in the middle, slightly to indistinctly 4-angled, round when viewed from below, longitudinally indistinctly fluted above; lobes  $2.5\text{--}4.0 \times 3\text{--}4$  mm, mostly white or pale yellowish green, fading pinkish brown when spent, broadly ovate, acute to nearly obtuse, sometimes apiculate. *Stamens* 8, inserted in the middle of the corolla tube, 1–2 mm exserted; filaments  $\pm 6$  mm long, thin, light greenish white; anthers  $\pm 0.5$  mm long, brownish orange. *Pistil* consisting of 4 carpels; carpels 6–8 mm long, light yellowish green; styles 2–4 mm long; stigmas shortly exserted, very slightly capitate, light yellow; scales  $\pm 2$  mm long, square to transversely oblong. *Follicles* 9–10 mm long, with the appearance of a grass spikelet, enveloped by dark brown, dry corolla tube, dull light green. *Seeds*



FIGURE 10.—The crested form of *Kalanchoe luciae* with narrowly oblong, marginally in-rolled leaves is known under the moniker *K. luciae* 'Oricula'. Photograph: G.F. Smith.

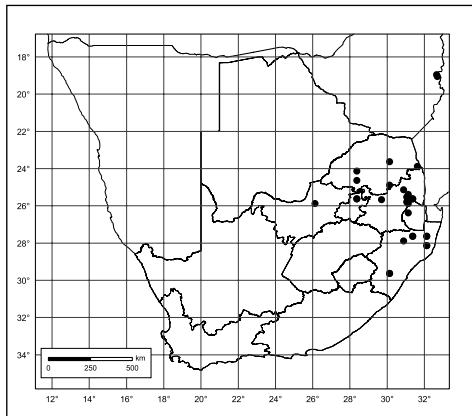


FIGURE 11.—Natural geographical distribution range of *Kalanchoe luciae* in southern and south-tropical Africa.

1.0–1.5 mm long, oblong, light brown. *Chromosome number*: unknown. Plate 2387.

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PLATE 2388 *Kalanchoe neglecta*

*Kalanchoe neglecta*

Crassulaceae: Kalanchooideae

*Southern Africa (South Africa, Mozambique)*

**Kalanchoe neglecta** Toelken in Journal of South African Botany 44: 90 (1978); Tölken: 63 (1985); Van Wyk & Smith: 93, Figure 193 (2001); Descouings: 167 (2003); Smith & Crouch: 85, figure at bottom of page (2009); Smith et al.: 311, figure at bottom of page (2017); Smith et al.: 201 (2019). *Kalanchoe rotundifolia* (Haw.) Haw. f. *peltata* Raym.-Hamet ex Fernandes: 208 (1978); Fernandes: 62 (1983).

The floristic treatments of the Crassulaceae, the *plakkie* family, including those of *Kalanchoe* Adans. and *Bryophyllum* Salisb. as a kalanchooid segregate (Crassulaceae subfam. Kalanchooideae emend. Gideon F.Sm.; see Smith & Monro (2022a, b) for the nomenclature to be used for this subfamily), for the regions covered by the *Conspectus florae angolensis* (Angola) and *Flora zambesiaca* (FZ) projects (Botswana, Zambia, Zimbabwe, Malawi, Mozambique), were published in quick succession by Fernandes (1982) and Fernandes (1983), respectively. This afforded Fernandes the opportunity to compare herbarium collections of *Kalanchoe* across a broad, contiguous swathe of Africa south of the equator, from Angola in the west to Mozambique in the east. The insights she gained into the taxonomy of the genus also enabled her to, earlier, have published a further major work on *Kalanchoe* (Fernandes 1980). Rosette Mercedes Saraiva Batarda Fernandes (1 October 1916 [Redondo, Portugal]–28 May 2005 [Coimbra, Portugal]) (Figure 1), who worked at the University of Coimbra, Portugal (Coutinho 2007), was the most prolific Portuguese taxonomist in terms of publishing new plant names in the 20th century (Figueiredo et al. 2018).

The Malagasy *Bryophyllum*, as *K.* subg. *Bryophyllum* (Salisb.) Koord., is nowadays treated as one of four subgenera recognised in *Kalanchoe* (see Smith 2022a), the other three being the autonymic, geographically widespread *K.* subg. *Kalanchoe*; as well as *K.* subg. *Alatae* (Raym.-Hamet) Gideon F.Sm., Shtein & D.-P.Klein (see Smith et al. 2021a); and *K.* subg. *Kitchingia* (Baker) Gideon F.Sm. & Figueiredo (see Smith & Figueiredo 2018; Smith et al. 2021b). Three of these four subgenera, *K.* subg. *Alatae*, *K.* subg. *Bryophyllum*, and *K.* subg. *Kitchingia*, are endemic to Madagascar. *Kalanchoe* subg. *Fernandesiae* Gideon F.Sm. from southern and south-tropical Africa, is here interpreted at the rank of section in *K.* subg. *Kalanchoe*, as *K.* sect. *Raveta* Raym.-Hamet ex Gideon F.Sm. (Smith 2020b; Smith 2022b, c). *Kalanchoe neglecta* (Figure 2), the subject of this paper, is a representative of *K.* subg. *Kalanchoe*, with this being the only subgenus represented naturally in southern Africa.

Apart from her work on *Kalanchoe* and *Bryophyllum*, Fernandes additionally expressed views on the taxonomy of other crassuloid species from the *Flora of Southern Africa* (FSA) region (Namibia, Botswana, Eswatini, Lesotho, South Africa). At the time Hellmut Richard Toelken (1 September 1939 [Windhoek, Namibia]– ) worked on the Crassulaceae treatment

PLATE 2388.—1, vegetative branch,  $\times 1$ ; 2, inflorescence,  $\times 1$ ; 3, apical view of corolla lobes,  $\times 6$ ; 4, lateral view of flower,  $\times 6$ ; 5, adaxial view of leaf showing peltate base,  $\times 1$ . Voucher specimen: G.F. Smith 1145 in H.G.W.J. Schweickerdt Herbarium (PRU), Pretoria. Artist: Lesley Deyssel.



FIGURE 1.—Rosette Batarda Fernandes (1916–2005) photographed at the age of 51. In 1982 and 1983 Rosette Fernandes authored the treatments of the Crassulaceae, including of *Kalanchoe* and *Bryophyllum*, for the *Conspectus florae angolensis* and *Flora zambesiaca* projects, respectively. Photograph kept in the private collection of Dr António Coutinho, University of Coimbra, Portugal. Reproduced with his permission.

for the FSA project. Inevitably there are differences between their treatments of the family for these abutting, and overlapping (Botswana), geographical areas. For example, Fernandes (1983) recognised *Cotyledon oblonga* Haw. at species rank, while Tölken (1985) treated it at the rank of variety, as *C. orbiculata* L. var. *oblonga* (Haw.) DC.

*Kalanchoe neglecta* is quite appropriately named: the specific epithet is derived from the Latin word *neglectus* (neglected), in reference to the several decades it took before a name was validly published for it at the rank of species (Tölken 1978). In that same year, Fernandes (1978) rather treated the species at the rank of forma under *K. rotundifolia* (Haw.) Haw. and used the epithet *peltata* at that rank, as *K. rotundifolia* f. *peltata*. Use of the epithet *peltata* at the rank of forma was earlier proposed by Raymond-Hamet (1960) for this entity, but he did not validly publish it (Smith 2020a). By the time that first Tölken (1978) and shortly afterwards Fernandes (1978) formally published names for the species, at two different ranks, it had already been known for over 30 years; it had been first

collected in 1948 by the Roman Catholic missionary Dr Father Jacob Gerstner (6 December 1888, Augsburg, Bavaria–October 1948, Zambia). This collection was made near Hlabisa in KwaZulu-Natal, on 15 May 1948, some five months before Gerstner died in Zambia at the age of 59 (Gunn & Codd 1981). Gerstner's specimen, *J. Gerstner 6871*, would become the type of the name *K. rotundifolia* f. *peltata*, while *J. Vahrmeijer & H.R. Tölken 83* is the type of the name *K. neglecta*, with both specimens held in the National Herbarium (PRE), Pretoria. Later, when treating *Kalanchoe* for the FZ project, Fernandes (1983) maintained her view that *K. neglecta* should be synonymised with her *K. rotundifolia* f. *peltata* (Fernandes 1978), an interpretation that is not currently upheld.

If *neglecta* was a good choice to use in the name for the southern African species treated here, at the rank of species the epithet *peltata* would indeed have been equally fitting, but it had already been used in *Kalanchoe* for the Malagasy species *K. peltata* Baill. and was therefore not available. At maturity, the leaves of *K. neglecta* are basally distinctly peltate, with the basal portion of the leaf blades being conspicuously up-turned (Figure 3). This has given rise to common names for the species that reference its leaf morphology, such as *sambreelkalanchoe* in Afrikaans, umbrella kalanchoe in English, and *iDlebe lenkau* (meaning 'monkey's ear') in isiZulu.

Species of *Kalanchoe* with peltate leaves are quite common and found in several taxa from Madagascar, for example *K. daigremontiana* Raym.-Hamet (Smith & Shtein 2021a) and *K. laetivirens* Desc. (treated as *K. ×laetivirens* by Smith [2020c]; see Shtein et al. [2021]), both included in *K.* subg. *Bryophyllum*, and in the East African *K. nyikae* Engl. (Smith & Figueiredo 2020), a species included in *K.* subg. *Kalanchoe*.

The large, often peltate leaves of *Kalanchoe neglecta* that somewhat resemble those of the very widespread northern hemisphere crassuloid species *Umbilicus rupestris* (Salisb.) Dandy (Smith & Figueiredo 2011), commonly known as navelwort, and even the leaves of the commonly grown nasturtium (*Tropaeolum majus* L., family Tropaeolaceae, *kappertjie* in Afrikaans), separate this species from its closest relatives among the species that have affinities with *K. rotundifolia*. However, *K. neglecta* is usually a much more robust species with a strong, thick, albeit herbaceous stem that can be up to 20 mm in diameter basally (Figures 1 and 3). Individual stems of this species, however, remain green and do not turn brown until after they have produced an inflorescence and, once reproductively redundant, wither and die. In the case of *K. rotundifolia*, perennial stems can remain green for a long time, after which they become somewhat brittle-woody, but in many cases do not die.

Not many kalanchoes develop thick roots. However, in the case of *Kalanchoe neglecta* the rootstock is robust and considerably thickened (Figure 4), and serve as a perennating organ from which new growth arises post-flowering in spring.

During the development of the terminal inflorescence of *Kalanchoe neglecta*, the flower clusters are distinctly protected by large sterile bracts that cat claw-like envelop the buds (Figure 5). At anthesis the inflorescences of *K. neglecta* are usually much more robust and usually more densely flowered than in *K. rotundifolia* (Figure 6). However, the diurnal flowers of *K. neglecta* are very similar to those of *K. rotundifolia*, but the free corolla lobes are generally slightly more slender and orange to yellowish orange. As is the case with



FIGURE 2.—*Kalanchoe neglecta* is one of the few southern African species of *Kalanchoe* that has distinctly peltate leaves. The stems of the species are round in cross-section and remain herbaceous for a long time. Photograph: G.F. Smith.



FIGURE 3.—The leaf blades of *Kalanchoe neglecta* are often saucer-like folded upwards along margins that can be very slightly red-infused. Photograph: G.F. Smith.



FIGURE 4.—The thickened, even slightly woody, rootstock of *Kalanchoe neglecta* serve as a perennating organ. Photograph: G.F. Smith.



FIGURE 5.—During the development of the inflorescence of *Kalanchoe neglecta* the flower clusters are distinctly protected by large, sterile, bract-like leaves that cat claw-like cover the buds. Photograph: G.F. Smith.

the corollas of *K. rotundifolia* post-anthesis, those of *K. neglecta* also become tightly twisted around the follicles as they dry out (Figure 7). *Kalanchoe neglecta* flowers in the comparatively dry autumn and winter months, from March to July, peaking from May to June (southern hemisphere) (Smith 2022d).

As presently understood, *Kalanchoe neglecta* is naturally restricted to the northeastern-most corner of the KwaZulu-Natal Province of South Africa and the adjacent southern parts of Mozambique around Bela Vista, so making it an endemic of the Maputaland Centre of Endemism, which is part of the Maputaland-Pondoland Region of Endemism (Figure 8). In this area it has been recorded from, inter alia, the Phinda Private Game Reserve, which forms part of the iSimangaliso Wetland Park (previously Greater St Lucia Wetland Reserve) (Olver et al. 2001). The species usually grows in small clusters in sandy soils not far from the Indian Ocean coast. With an estimated 7 000 indigenous plant species, Maputaland is one of the richest floristic areas in Africa (Van Wyk & Smith 2001; see also Bruton & Cooper (1980) on the ecology of Maputaland); for a more broadly defined eastern region of South Africa 10 000 species have been recorded (Pooley 1998). *Kalanchoe neglecta* is not threatened and it is included in the Red List category of Least Concern (Smith et al. 2022).

Although virtually unknown in cultivation, *Kalanchoe neglecta* is easy to grow. Seed of *K. neglecta* germinates readily and can be sowed in seedling trays that at least initially should be watered from below by standing the tray in a large saucer filled with water. When the seedlings are about 50 mm tall they can be pricked out and planted directly in the garden where they

are intended to grow. The stems of this species are somewhat brittle and fragile and care should be taken when handling them when seedlings are transplanted. Alternatively, plantlets that sprout at the base of a flowering stem can be removed with a sharp knife, left



FIGURE 6.—Inflorescence of *Kalanchoe neglecta* viewed from above. Photograph: G.F. Smith.

in the shade for a few days to allow the wound to dry, and rooted directly in the place where plants are desired; plants do well in containers and in open beds. Plants will grow and thrive in virtually any soil type, but do best in a friable, well-drained soil mixture. They thrive in dappled shady positions, where they will develop to flowering maturity within one or two seasons. Leaf cuttings, with the petiole intact, do not readily strike root; this is a common reproductive strategy in some infrageneric groups of *Kalanchoe* (Smith et al. 2021c). Rather, in the case of *K. neglecta*, the severed end of the petiole produces callus-like tissue that seems to act as a wound sealant, rather than as a progenitor of root primordia.



FIGURE 7.—Close-up of the orangey yellow flowers of *Kalanchoe neglecta*. The upper half of the corolla tube, as well as the corolla lobes, become tightly twisted post-anthesis. The flowers of this form of the species are distinctly orange. Photograph: G.F. Smith.

Leaf carunculations were recently reported from several specimens of *Kalanchoe neglecta* (Smith & Shtein 2021b). The carunculations, when present, are generally very prominent and have the appearance of small, tubular towers (Figure 9a), or are low and rounded and appear as prominent corrugations on the adaxial surface of the leaf blade (Figure 9b). Not all specimens of this species had this leaf trait and it appears to be under

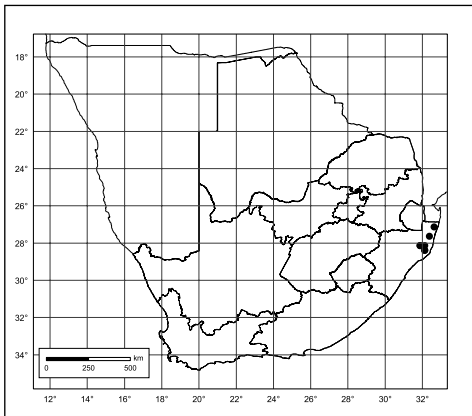


FIGURE 8.—Known natural geographical distribution range of *Kalanchoe neglecta* in southern Africa. The species also occurs in southern Mozambique.

genetic control, at least to some extent. In the Crassulaceae, for example in the New World *Echeveria gibbiflora* DC. (Crassulaceae subfam. Sempervivoideae), the development of deviant leaf surface outgrowths is well-known and often exploited in selecting material for a gardening public eager to obtain ‘new’ plants. Such leaf outgrowths are most commonly referred to in the vernacular as carunculations (Kimmach 2003). Material with such leaf surface aberrations is variously also referred to as being ‘blister-leaved’ (Walther 1972 [under *E. grandifolia* Haw., which Walther (1972: 207–208) upheld in addition to *E. gibbiflora*]; Pilbeam 2008); as having ‘gibbous protuberances’ (Carruthers & Ginns 1973); or as being ‘bumpy’ (Schulz & Kapitany 2005; Moore 2017); and the structures

themselves are also called ‘excrecences’ (Pilbeam 2008) – see Smith & Shtein (2021b) for a discussion. Resende & Viana (1965) used the term ‘crests’ for the irregular, variously lumpy tissue that developed on the leaves and sometimes also on the petioles of representatives of *Kalanchoe* that they investigated at the University of Lisbon, Portugal. To prevent confusion with fasciated plant material, the irregular growth found on the leaves of *K. neglecta* investigated is here referred to as ‘carunculations’ (Smith & Shtein 2021b).

**Description.**—Perennial, few-leaved, usually unbranched, glabrous, small to medium-sized succulent, to 1.2 m tall. *Rootstock* robust, considerably thickened. *Stems* green, somewhat brittle, few, arising from herbaceous to slightly woody base, erect to leaning. *Leaves* opposite-decussate, petiolate, light green, succulent, spreading, papery on drying; petiole 20–80 mm long, not channelled above, not stem-clasping; blade 40–120 × 30–80 mm, broadly elliptic, ovate, cordate or peltate, saucer-like folded upwards along margins, adaxial



FIGURE 9.—Adaxial surface of a leaf of *Kalanchoe neglecta*: a, showing tubular carunculations; b, showing low, rounded carunculations. Photographs: G.F. Smith.

leaf surfaces smooth or with carunculations of various shapes and sizes; base deeply cordate in lower leaves, usually cuneate in young leaves; apex rounded-obtuse; margins entire or coarsely crenate or undulate-crenate into rounded, harmless, patelliform crenations. *Inflorescence* a flat-topped, many-flowered thyrse with several dense dichasia, to 600 mm tall, erect to leaning, usually apically dense, more rarely sparse, rather round in outline when viewed from above, branches opposite, lacking leafy branchlets in axils, axis green to bluish-green; pedicels 4–7 mm long, slender. *Flowers* erect; calyx consisting of four sepals; sepals 2–3 mm long, light green, elongated-triangular, acute, separate, basally slightly fused, curved away from base of corolla tube, hardly contrasting against green part of corolla tube; corolla 6–8 mm long, distinctly enlarged lower down around carpels, distinctly and tightly twisted apically after anthesis; tube 5–7 mm long, upper half to quarter of tube orange to yellowish orange, gradually becoming light green-infused in lower half to two-thirds or sometimes as much as three-quarters of tube, globose-rounded, indistinctly 4-angled, longitudinally distinctly narrowing above carpels; lobes  $2.5\text{--}3.0 \times 1.5\text{--}2.0$  mm, orange to yellowish orange, same colour as upper half of tube, orange more intense towards the lobe margins, lanceolate, distinctly acute apically, spreading. *Stamens* included; filaments thin; anthers 0.5–0.7 mm long. *Pistil* consisting of 4 carpels; carpels 6–7 mm long, mid-green; styles short; stigmas very slightly capitate; scales  $\pm 2$  mm long, narrowly tapering, linear. *Follicles* enveloped in dry, dark brownish-purple remains of corolla, 6–7 mm long, drying dark brown, sharply recurved like a peeled banana at tips. *Seeds* 0.8–1.0 mm long, dark brown. *Chromosome number*: unknown. Plate 2388.

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*Kalanchoe orgyalis*

Crassulaceae: Kalanchooideae

Madagascar

***Kalanchoe orgyalis*** Baker in Journal of Botany, British and Foreign, London 20: 110 (1882); Hamet: 890–891 (1907); Hamet: 47 (1908); Hamet: 127–133 (1915); Berger: 407 (1930); Raymond-Hamet & Marnier-Lapostolle: 67, Plate XXV, Figure 80, 81 (1964); Jacobsen: 288 (1977); Jacobsen: 622, Figure 874 (1986); Sajeve & Costanzo: 153 (1994); Boiteau & Allorge-Boiteau: 140–142 (1995); Rauh: 237 (1995); Rauh: 303, 312, Figure 1154–1156 (1998); Descoings: 168 (2003). *Kalanchoe antanosiana* Drake del Castillo: 41 (1903); Hamet: 891 (1907); Hamet: 45 (1908); Raymond-Hamet: 127–133 (1915); Raymond-Hamet & Perrier de la Bâthie: 167–170 (1914); Jacobsen: 288, as *K. antonasyana* [sic] (1977); Jacobsen: 606, as *K. antonasyana* [sic], 622 as *K. cantonasyana* [sic] (1986).

In 1869, John Gilbert Baker (3 January 1834, Guisborough, North Yorkshire, United Kingdom–16 August 1920, Kew, Richmond, United Kingdom) (Figure 1) was appointed as the first assistant at the Herbarium of the Royal Botanic Gardens, Kew. He was an accomplished naturalist and prolific author, and eventually rose to the position of Head of the Library and Curator of the Kew Herbarium, a post he held from 1890 to 1899. During the 1880s Baker was provided with large volumes of often undescribed plant material that was collected in Madagascar by, inter alia, the Reverend Richard Baron (8 September 1847, Kendal, Westmorland, United Kingdom–12 October 1907, Morecambe, Lancashire, United Kingdom) (Figure 2). Over a period of several years, Baker described many new genera and species represented by Baron's specimens (see for example Baker 1881, 1883, 1884, 1887). Among these were several new species of *Kalanchoe* sensu lato Adans. (Crassulaceae subfam. Kalanchooideae) and one of these was a yellow-flowered species for which he published the name *K. orgyalis* (Baker 1882). As part of the description, Baker cited two gatherings, both of which were collected in Madagascar by Reverend Baron, who was a missionary with the London Missionary Society, an interdenominational evangelical missionary society that was formed in England in 1795. Baron eventually spent about 35 years on the island, where he made extensive collections of plants (Dorr 1997; Smith & Figueiredo 2021a). Baron was also a proficient naturalist (Dorr 1997), an interest that seemingly often went hand-in-hand with missionary work (Dorr 2019). From 1871 to 1877, Henrietta Baker (4 April 1831, Castleton, Yorkshire, England–19 June 1913, Levenshulme, Manchester, England), a relative of John G. Baker, was also a missionary in Madagascar, and Dorr (1997) speculates that she might have been instrumental in encouraging British missionaries, likely including Richard Baron, to collect plants in Madagascar. Dorr (1992) further notes that Baron's second wife encouraged him in his botanical interests.

Baron had several notable natural history achievements, including publishing the first botanical textbook on botany in Malagasy, and his *Compendium des Plantes Malgaches* that appeared between 1900 and 1906 was the first complete catalogue of the vascular plant

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PLATE 2389.—1, vegetative branch (background),  $\times 0.8$ ; 2, inflorescence (foreground),  $\times 0.8$ ; 3, apical view of corolla lobes,  $\times 6$ ; 4, lateral view of flower,  $\times 6$ . Voucher specimen: G.F. Smith 1125 in H.G.W.J. Schweickerd Herbarium (PRU), Pretoria. Artist: Lesley Deysel.



PLATE 2389 *Kalanchoe orgyalis*



flora of Madagascar (Dorr 1987, 1997). Herbarium material – an estimated 12 000 specimens, which probably includes duplicates – that Baron collected in Madagascar was mostly sent to the Royal Botanic Gardens, Kew, where the novel material, conceivably as many as 1 000 species, was described, chiefly by John G. Baker (Dorr 1987). Reverend Baron additionally took on the editorship of *The Antananarivo Annual* from 1881 until 1883, and thereafter was co-editor of this journal, along with James Sibree (Dorr 1992), who was also employed by the London Missionary Society. Despite this journal being little-known, it contains ‘an important amount of botanical information, especially that which concerns botanical exploration, ethnobotany, and the common names of plants in Madagascar’ (Dorr 1992).

When Baker (1882) described *Kalanchoe orgyalis* he cited two Baron collections, namely *Baron 105* and *Baron 249* (Smith & Figueiredo 2022a). Almost 50 years later when Stearn (1931a) published the name *K. aleurodes* Stearn, he compared this Zimbabwean species to the Malagasy *K. orgyalis* (Smith & Figueiredo 2021b, 2022b). With the knowledge of hindsight, it is somewhat perplexing that Stearn (1931a, b) compared his *K. aleurodes* to *K. orgyalis* as the two species have very different morphologies (Tutin 1931; Smith & Figueiredo 2021b). However, at the time, *K. orgyalis* was not yet well understood (see below for a discussion of *K. antanosiana* Drake with reference to *K. orgyalis*) and given the vaguely similar reproductive morphologies of *K. aleurodes* and *K. orgyalis*, comparing them must have made sense to Stearn.

Just more than 20 years after Baker (1882) published the name *Kalanchoe orgyalis* based on Baron’s preserved herbarium collections numbered 105 and 249, the French botanist Emmanuel Drake del



FIGURE 1.—Portrait of John Gilbert Baker (1834–1920) who published the name *Kalanchoe orgyalis*. Reproduced from *Journal of Botany, British and Foreign*. London, volume 39 (1901). Photograph: Berthold Carl Seemann, public domain ([http://www.plantillustrations.org/illustration.php?id\\_illustration=176522](http://www.plantillustrations.org/illustration.php?id_illustration=176522)).



FIGURE 2.—Portrait of Reverend Richard Baron (1847–1907) who collected the material on which Baker based the name *Kalanchoe orgyalis*. Credit of the photograph is to Fiangonan’i Jesoa Kristy eto Madagasikara (FJKM), which is the lineal descendent of the London Missionary Society, Antananarivo, that employed Baron. Permission was granted to Dr Laurence J. Dorr by FJKM to disassemble a framed collection of photographs of 19th century missionaries to obtain individual portraits for use in Dorr (1997).

Castillo (1855–1904) published the name *K. antanosiana* for material that was collected by Guillaume Grandidier (1873–1957) on 19 May 1898 in the Vallée du Saint-Augustin in southwestern Madagascar (Toliara Province) (Smith & Figueiredo 2022c). Grandidier collected this material on his first expedition to the island that lasted from 1898 to 1899 (Drake del Castillo 1903; Dorr 1997). The specimen on which Drake del Castillo based the name *K. antanosiana* is *G. Grandidier s.n.* (P00374220), which is held in the Paris Herbarium. This specimen is clearly representative of what is today known as *K. orgyalis*. Note that in 1888, when Guillaume Grandidier was only 15 years old, *K. grandidieri* Baill. was named for his father, Alfred Grandidier (1836–1921), who, earlier, also collected in Madagascar.

While Drake del Castillo worked on Grandidier's Malagasy collections in the early 1900s, the then still early-teenaged Raymond Hamet (1890–1972), was independently working on *Kalanchoe* with a view to revise the genus (Smith 2020). Perhaps rather surprisingly, Hamet seems to have been unaware of or, at least in some respects, misinterpreted the new *Kalanchoe* species described in Drake del Castillo (1903). This is *inter alia* evidenced by Hamet having described *K. tieghemii*, as '*Tieghemi*', only three years after Drake del Castillo published the name *K. beharensis* for this commonly cultivated species (Smith et al. 2021).

Hamet (1907, 1908, 1915) as well as Raymond-Hamet & Perrier de la Bâthie (1914) regarded *Kalanchoe orgyalis* and *K. antanosiana* as two distinct species (see for example species numbers 15 and 16 in Hamet's two-part monograph of 1907 and 1908). The celebrated French botanist Jean-Henri Humbert (1887–1967), who amassed a remarkable 50 000 herbarium specimens, collected in various parts of the world, during a long and productive botanical career (Figueiredo & Smith 2021), added a determinavit strip dated '1915' to the type of the name *K. antanosiana* on which he suggested that this species of Drake del Castillo belongs in the synonymy of *K. orgyalis*. Humbert had more than a passing interest in *Kalanchoe* (see for example Humbert 1933a, b; Guillaumin & Humbert 1941; Shtein et al. 2021), and *K. antanosiana* was eventually indeed formally synonymised under *K. orgyalis*, for example in Jacobsen (1977: 288, as *K. antonasyana* [sic], 1986: 606, also as *K. antonasyana* [sic] and on p. 622 as *K. cantonasyana* [sic]). This view was followed in Boiteau & Allorge-Boiteau (1995) and in Descoings (2003), the latter being the most recent global-level treatment of the genus.

From both vegetative and reproductive perspectives it is easy to identify *Kalanchoe orgyalis*: plants are shrubby and can reach a height of well over 1 m (Figure 3); the adaxial leaf surfaces are copper-coloured and have a felt-like texture (Figure 4); the sepals are short, stubby, bright green and very succulent (Figure 5); the corolla tubes are urceolate and bright yellow to bright lemon yellow (Figure 6); and the fruit are small, dark brown to almost black and looks like currant grapes (Figure 7). Of these characters the one that mostly contributed to *K. orgyalis* becoming very popular in gardening circles in mild climates is the copper-coloured leaves. Given the spatulate leaf outline, plants are mostly sold in nurseries as *K. 'Copper Spoons'*, i.e., with '*Copper Spoons*' used as what appears to be a cultivar name, but also as a common name. In Afrikaans *K. orgyalis* is known as *koperkalanchoe* or *koper lepels*, again references to the copper-coloured leaves. The vernacular Malagasy name recorded by Baker (1882) for *K. orgyalis*, *Hazombato*, was also included in Richardson (1885), a Malagasy-English dictionary. *Hazombato* is additionally used for 'a [presumably

any] tree whose wood is used in house building' (Richardson 1885). Note though that the rather thin and herbaceous-woody stems of *K. orgyalis* hardly can be considered to be of any use in construction.

*Kalanchoe orgyalis*, which is at present included in *K. subg. Kalanchoe*, does not present undue challenges in cultivation and in time will grow into a handsome, medium-sized to large, multi-branched shrub. If kept in a container, for example in a greenhouse in places with a harsh, continental-type climate, plants will remain small, rather sparsely branched and somewhat stunted for many years, but may not flower for a long time (Figures 8 and 9). Even when grown outdoors in open beds, plants can take a few years before flowering is initiated. Propagation of the species is easy as plants grow readily from stem cuttings and severed leaves (Figure 10), or even from leaf fragments, or, as noted by Jacobsen (1986), plants may even develop plantlets on leaves that are still attached to the plant, especially if the leaves have been damaged, for example in a hail storm. However, unlike *K. beharensis*, one of its woody-stemmed relatives, *K. orgyalis* does not have invasive tendencies (Walters et al. 2011; Smith et al. 2019, 2021).

Where cultivated and flowering in southern Africa, *Kalanchoe orgyalis* is often visited by sunbirds (family Nectariniidae). Especially the White-bellied Sunbird, *Cinnyris talatala* (A. Smith, 1836) has been observed to feed on the nectar contained in the bright yellow to bright lemon yellow, short-tubular flowers of *K. orgyalis* (Figure 11). *Cinnyris talatala* has been recorded from northern and eastern South Africa, Eswatini (formerly Swaziland), Mozambique, Malawi, Botswana, Zambia, southern Angola and to as far north as Tanzania (Skead 1967; Hockey et al. 2005). *Kalanchoe orgyalis* flower in winter and spring



FIGURE 3.—Plants of *Kalanchoe orgyalis* are perennial, medium-sized to large shrubs, and usually densely branched. Photograph: G.F. Smith.



FIGURE 4.—The upper surfaces of the spoon-shaped leaves of *Kalanchoe orgyalis* are covered in a very fine, golden-brown to copper-coloured tomentum, especially when the leaves are young. The lower surfaces are silvery white to dull green. The leaf in the centre is uncharacteristically heart-shaped. Note that the petioles are distinctly grooved above, so effectively channelling rain and water condensate to the stems and ultimately the roots. Photograph: G.F. Smith.



FIGURE 5.—The bright green, thickly succulent sepals of *Kalanchoe orgyalis* are short, stubby and pointed. Photograph: G.F. Smith.

with a peak from August to September (southern hemisphere). As is the case with many kalanchoes, flowers may occasionally be produced well into summer (Figure 12).

When referring to the specific epithet *orgyalis* used in the name *Kalanchoe orgyalis*, Boiteau & Allorge-Boiteau (1995) stated that: ‘orgyalis vient d’un mot grec qui veut dire « long au bout d’une brasse », i.e., that the epithet comes from a Greek word that refers to a measure of six feet, the length of two outstretched arms. In the protologue of the name *K. orgyalis* the length of the stems are given as ‘6–7 feet’, with the species therefore having been named for the height of the plant.

As far as we are aware the accompanying plate is the second botanical painting that is published of *Kalanchoe orgyalis* in the past 30 years. The first one appeared in Boiteau & Allorge-Boiteau (1995). The



FIGURE 6.—The corolla tube as well as the corolla lobes of *Kalanchoe orgyalis* are virtually uniformly bright lemon yellow, sometimes more intensely so lower down. Photograph: G.F. Smith.

work of Boiteau & Allorge-Boiteau (1995) was a treatment of *Kalanchoe* in Madagascar, with most species essays included in it being illustrated with paintings rather than photographs. This prompted Dorr (1998) to remark 'that the botanical artist plays a much more useful and instructive role in plant taxonomy than does the botanical photographer', when the plates are compared to the colour photographs included in the book of Boiteau & Allorge-Boiteau (1995).

*Kalanchoe orgyalis* occurs naturally in south-central and southern Madagascar (Boiteau & Allorge-Boiteau 1995; Rauh 1995) (Figure 13). The location from where the type material of the name *K. orgyalis* originated was recorded as 'West Betsileo, on stony ground and about woods' (Baker 1882). However, 'Betsileo' does not reference a place; rather, 'Betsileo' refers to an



FIGURE 7.—With age, the fruit of *Kalanchoe orgyalis* have the appearance of small, blackcurrant grapes. Photograph: G.F. Smith.



FIGURE 8.—A potted specimen of *Kalanchoe orgyalis* (copper-coloured plant in the centre) offered for sale in the garden shop of the Missouri Botanical Garden in St Louis, Missouri, U.S.A. Photograph: G.F. Smith.



FIGURE 9.—*Kalanchoe orgyalis* (copper-coloured leaves) growing to the right of *K. luciae* in the tub-shaped container in the centre of this potted display in the Denver Botanical Garden, Colorado, U.S.A. Photograph: G.F. Smith.



FIGURE 10.—A plantlet of *Kalanchoe orgyalis* sprouting from the proximal end of a severed leaf. Photograph: G.F. Smith.

ethnic group that occupies the southern part of the central plateau of Madagascar (L.J. Dorr, personal communication). Most of the territory occupied by the Betsileo falls in the Fianarantsoa Province of Madagascar, where the provincial capital of the same name is situated. The material of *K. orgyalis* was one of the early collections of Reverend Baron while he lived in the city of Fianarantsoa.

**Description.**—Perennial, medium-sized to large shrubs, usually much and densely branched, succulent, variously clothed in a very fine, copper brown tomentum, 1–2 m tall. *Stems* opposite-branched, herbaceous to, later, somewhat woody, comparatively terete,  $\pm$  erect or variously leaning outwards, surface greyish white lower down, silvery white higher up, finely cracked, leaf scars obvious. *Leaves*



FIGURE 11.—*Cinnyris talatala*, the White-bellied Sunbird, feeding on the nectar in the yellow, short-tubular flowers of *Kalanchoe orgyalis*. Photograph: G.F. Smith.

decussate, spatulate, rather laxly arranged, few to many especially towards terminal half to three-quarters of branches, tightly attached to branches, slowly shed lower down to yield small, but rather conspicuous brownish black leaf scars, erect when young to variously spreading at maturity, succulent, covered in a very fine, golden-brown to copper-coloured tomentum, petiolate; petiole 5–18(–20) mm long, narrowly cylindrical, prominently 1-grooved adaxially, fleshy to slightly woody, not enlarged where attached to stem; blade 50–150 × 40–80(–100) mm, abaxially silvery white to dull green, adaxially golden-copper especially when young, to dull green later, ovate to nearly round to somewhat ovate-lanceolate, succulent, flat to slightly concave above, flat to slightly convex below; base attenuate to truncate; margins slightly oyster shell-like turned up, concolorous; apex somewhat abruptly acute-tipped, rarely indented apically. *Inflorescence* a rather dense, corymbose cyme, somewhat laxly branched, few- to many-flowered, up to (0.45–)0.50–1.00(–1.10) m tall, somewhat pyramidal, erect to gracefully leaning sideways and bending upwards, branches horizontal to obliquely slanting



FIGURE 12.—Like many kalanchoes, the predominantly winter-flowering *Kalanchoe orgyalis* may occasionally produce scattered flowers well into summer. This photograph was taken in December, in midsummer (southern hemisphere). Photograph: G.F. Smith.

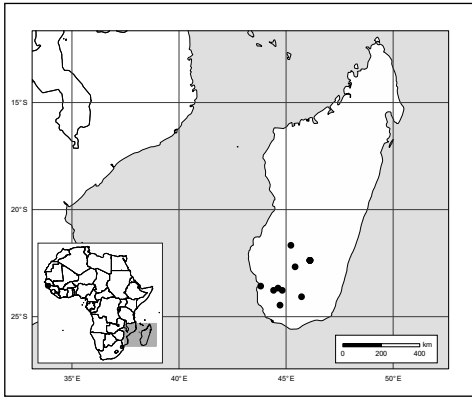


FIGURE 13.—Geographical distribution range of *Kalanchoe orgyalis* in south-central and southern Madagascar based on verifiable information held in the Global Biodiversity Information Facility and specimens cited in Boiteau & Allorge-Boiteau (1995) that was used for Map 13 reproduced in that work, and Map 14 reproduced in Allorge-Boiteau (1996).

upwards; pedicels 5–12(–15) mm long, coppery silver, usually sturdy, widening towards base of flower. *Flowers* 4-merous, rarely 5-merous,  $\pm$  erect or slanted in various directions, smooth or sometimes very finely pilose, waxy bloom absent, narrowing towards the mouth; buds at first light greenish yellow especially towards tips, soon turning same colour as mature flowers; calyx bright light green, very obscurely infused with a network of reddish veins especially towards tip, very finely and irregularly pilose; sepals 3.0–5.5  $\times$  1.5–2.5 mm, deltoid-triangular, attached to the base of the corolla tube, thickly succulent, free, tube absent, bent away from the tube at a 90° angle, not connate, acute-tipped, much shorter than corolla tube; corolla consisting of four, rarely five, fused petals, tube and lobes virtually uniformly bright yellow to lemon yellow, more intensely yellow lower down and longitudinally along tube angles, very fleshy; tube (6–)12(–15) mm long, dis-

tingly quadrangular-urceolate to somewhat campanulate, tapering to a narrow mouth, distinctly fleshy, 4-angled; lobes 3–5  $\times$  1.5(–3.0) mm,  $\pm$  ovate to deltoid, lacking a distinct central keel, strongly recurved at maturity, not or rarely indented at tips, acutely cuspidate. *Stamens* inserted high up in corolla tube, of two lengths, included; filaments  $\pm$  2 and 3 mm long, thin, light yellow; anthers  $\pm$  1.0–1.5 mm long, hastate to ovate-oblong, yellow, included but visible at the mouth. *Pistil* consisting of four carpels; carpels 7–9 mm long, light yellowish green, distinctly globular enlarged, abruptly tapering upwards; styles 3–5 mm long, light yellowish green, slightly scabrid; stigmas hardly capitate, light yellowish green; scales  $\pm$  1.0–1.5  $\times$  1.5–2.5 mm, greenish yellow,  $\pm$  tooth-like, horizontally-rectangular, separate, not connate, slightly tapering upwards, uneven-rounded above. *Follicles* 6–7(–8) mm long, shiny light yellowish green to mid-green, remaining so for a long time, eventually becoming brittle, grass spikelet-like, tightly enveloped in dry, long-lasting, reddish brown to dark brown to almost black remains of corolla, ultimately variably turning dark brown to black, short, dried styles persistent. *Seeds* 0.5–0.6 mm long, dark brown to nearly black, rectangular-straight or banana-shaped-curved, slightly apiculate at one end, hardly longitudinally striated. *Chromosome number*:  $2n = \pm 72$ , a tetraploid (Uhl 1948; Friedmann 1971). Plate 2389.

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*Kalanchoe ×estrelae*

Crassulaceae: Kalanchooideae

*South Africa*

**Kalanchoe ×estrelae** Gideon F.Sm. in *Phytotaxa* 441(2): 225 (2020a); Smith: 322 (2020b); Smith: 43 (2021).

‘But the art of horticulture is not botany.’  
Rothschild et al. (2004: 78)

In the ‘Preface’ to the first volume of the then *The Flowering Plants of South Africa*, Dr Illtyd Buller Pole Evans (1879–1968) (Gunn 1971; Gunn & Codd 1981), at the time Director of the Division of Botany and Plant Pathology, stated that, ‘It is with the objective of bringing these gems of nature [the spectacular flora of South Africa] to the notice of the public that this publication is offered.’ (Pole Evans 1921: first unnumbered ‘Preface’ page preceding Plate 1). That first volume of what, in 1945, became *The Flowering Plants of Africa*, i.e., sans ‘South’, and later still simply *Flowering Plants of Africa (FPA)*, was published in 1921 and this year, 2023, i.e., 102 years later, the statement of Pole Evans holds true: the 2 400 botanical artworks that have appeared in the pages of this series attest to the magnificent floral diversity found in South Africa, further north on the African continent, as well as in Madagascar, the island off the east coast of Africa.

Almost 70 years after the first volume of *FPA* was published, Killick & Du Plessis (no date [1987]) stated in their Index to volumes 1 to 49, that, ‘showy plants not already figured are becoming increasingly difficult to find, so we sometimes figure [in *FPA*] botanically interesting but less showy plants’. However, this statement proved to be somewhat premature, because, during the past more than 30 years since that declaration was published, more than 400 additional botanical artworks of ‘gems of nature’ appeared in this series, i.e., what Pole Evans envisaged for inclusion in its pages in 1920 – the year in which he wrote the ‘Preface’ to volume 1 of the series.

The texts that accompanied the exquisitely beautiful artwork published in *FPA* during the first more or less 25 years were very much focused on formal descriptions as well as the origin of the material, with, often, minimal supplementary information provided on the plants illustrated. However, since 1945, when Dr R. Allen Dyer (1900–1987) assumed the editorship of *FPA* (Codd 1988), the texts that accompany the plates that grace this serial publication have increasingly become more comprehensive and scientifically robust, with, especially over the past ca. 30 years, these well-researched treatments being nothing short of mini monographs of the species treated. However, *FPA* is not intended to appeal only to

PLATE 2390.—1, inflorescence, × 1; 2, apical portion of a stem before inflorescence development is initiated, × 1. Voucher specimen: G.F. Smith 1145 in H.G.W.J. Schweickerdt Herbarium (PRU), Pretoria. Artist: Gillian Condy.



PLATE 2390 *Kalanchoe xestrelae*





FIGURE 1.—When grown in full sun, the leaves of *Kalanchoe xestrelae* take on a bright red hue, a popular colour among gardeners and horticulturalists for the foliage of succulent and other plants. The leaf margins of this form are almost entire. Photograph: G.F. Smith.

professional botanists. On the contrary, horticulturalists and gardeners are equally, if not more so, interested in the spectacular continental flora that has yielded so many botanical jewels that are today widely cultivated in gardens globally. South Africa has indeed given the world a multitude of indoor and outdoor plants that are today grown in far flung locations. Just think of agapanthi, aloes, mesembis, nerines, proteas, strelitzias and scores more.

Pole Evans (1921: first unnumbered ‘Preface’ page preceding Plate 1) further stated: ‘In recent years [...] it is becoming fashionable to have a rockery of aloes, vijgies [modern Afrikaans: vygies], and other succulents as one of the chief adjuncts of the garden.’ More than 100 years later, this statement has attained additional significance; with the advent of waterwise gardening – even no-irrigation gardening – succulents increasingly have become the mainstay of gardens in South Africa where water is at a premium.

*Kalanchoe xestrelae* Gideon F.Sm., which is included in Crassulaceae subfam. Kalanchooideae A.Berger emend. Gideon F.Sm. (Smith & Monro 2022a, b), the subject of this paper, is a leaf succulent, and a highly desirable one to cultivate at that, given its usually red to purplish-red leaves, a colour that horticulturally is often obsessed over (Figure 1). The multiplication sign preceding the specific epithet indicates that this is a hybrid. Over the years, hybrids, both natural and artificial, have indeed featured in some of the volumes of



FIGURE 2.—The soup plate-sized leaves of material of *Kalanchoe luciae* popularly sold under the moniker ‘Red Lobster’, are light green or glaucous, with a bright red to purplish red infusion. Photograph: G.F. Smith.

*FPA*, with *Haworthiopsis*  $\times$ *tauteae* (Archibald) Gildenh. & Klopper, illustrated as *Haworthia tauteae* Archibald, being one such example.

Four of the *Kalanchoe* species that are indigenous to southern Africa have significant outdoor horticultural appeal. Two of these, *K. luciae* Raym.-Hamet and *K. thyrsiflora* Harv. (Phillips 1929), have thick and heavy, paddle- or soup plate-shaped, i.e., round to obovate, and -sized leaves with smooth margins. The leaves of both species can be red- to reddish purple-infused – often heavily so in the case of *K. luciae* (Figure 2). This has given rise to both species having become popular as accent plants (Figure 3), but in some recent industrial-scale landscaping projects have also been planted in dense swathes over large areas to serve as a robust ‘groundcover’. After several years of vegetative growth, typically between three and five, both *K. luciae* and *K. thyrsiflora* produce tall, club-shaped inflorescences in winter, with the inflorescences densely flowered with small, cigar-shaped flowers with whitish corolla lobes in the case of *K. luciae* (Figure 4), and more cylindrical ones with yellow lobes in the case of *K. thyrsiflora*. Virtually all the plant parts, but especially the young growth as well as the inflorescences and flowers of both species, are densely covered in a sticky, white-waxy bloom (Smith 2020c; Smith & Figueiredo 2021).

Two further southern African kalanchoes, *Kalanchoe longiflora* Schltr. ex J.M.Wood (Smith & Figueiredo 2017) and *K. sexangularis* N.E.Br. (Tölken 1983; Figueiredo et al. 2016),



FIGURE 3.—*Kalanchoe luciae*: a, (foreground) grown as an accent plant in the Pretoria National Botanical Garden; b, a beautiful purple-leaved form of *Kalanchoe luciae* grown as a feature plant in a large garden. Photographs: G.F. Smith.

are very popular in horticulture in various parts of the world. However, unlike the leaves of the soup plate-leaved species discussed above, those of *K. sexangularis* and *K. longiflora* are much smaller, variously recurved and folded, and have margins that are irregularly toothed. All plant parts of *K. sexangularis* are additionally red-infused, with the red turning an intense crimson colour, especially in winter and when plants are grown in full sun in well-drained positions (Figure 5). In contrast, *K. longiflora* has turquoise-coloured leaves that become orange-infused in similar, exposed positions. Like virtually all kalanchoes, both species flower in winter and carry their yellowish green to bright yellow, narrowly urn-shaped, somewhat tubular flowers in tall, diffuse inflorescences that branch higher up (Smith et al. 2019).



FIGURE 4.—The inflorescences of *Kalanchoe luciae* are densely flowered and club-shaped in outline. The corolla lobes of this form are pure white. Photograph: G.F. Smith.



FIGURE 5.—The leaves of *Kalanchoe sexangularis* are almost invariably bright red-infused, especially when growing in exposed positions. Like most kalanchoes, plants flower during winter. Photograph: G.F. Smith.



FIGURE 6.—The slightly curved flowers of *Kalanchoe sexangularis* have a yellowish green corolla tube and bright yellow corolla lobes. Photograph: G.F. Smith.



FIGURE 7.—*Kalanchoe luciae* and *K. sexangularis* (right background) growing together. In a situation such as this, the hybrid, *K. ×estrelae* can easily arise once plants reach reproductive maturity. Photograph: G.F. Smith.

If a waterwise groundcover is desired, either *Kalanchoe longiflora* or *K. sexangularis*, or a combination of these two species, works very well, as, even when not in flower, the leaves of these two species provide horticultural interest because of their fantastically colourful foliage (Smith 2020d; Smith & Shtein 2021). Before reaching reproductive maturity, plants of both species are low-growing or of medium height – hardly exceeding 0.5 m – especially when grown in direct sunlight. The inflorescences of these two shrubs are carried on long, erect but often variously leaning peduncles on which small, yellow, erectly disposed flowers are usually densely arranged (Figure 6). Given how widely these two species are cultivated, they too have hybridised. This hybrid has also been described, as *K. ×hankeyi* Gideon F.Sm. [*K. longiflora* × *K. sexangularis*]. Like *K. ×estrelae*, the subject of this paper, *K. ×hankeyi*, too, has distinct horticultural potential (Smith 2020e).

Given the popularity of *Kalanchoe luciae* and *K. sexangularis* in South African horticulture and because they are often grown together (Figure 7), the two species have hybridised spontaneously with the hybrid at first recorded in Gqeberha in the Eastern Cape Province of South Africa, from where it was described as a cultivar (Bischofberger 2015). However, the hybrid has also arisen elsewhere in gardens, for example in Tshwane. To facilitate communication about it and to additionally provide opportunities to better study character inheritance, as well as character dominance, in *Kalanchoe*, the hybrid was described as *K. ×estrelae*.



FIGURE 8.—The bright red, branched plant on the left is representative of the form of *Kalanchoe xestrelae* here described as the cultivar ‘Fire Engine’. Photograph: G.F. Smith.

The presence of a dense, white-waxy substance on virtually all the plant parts of *Kalanchoe luciae* is one of the distinctive characters of the species, and other, similar ones for that matter, which are included in *K.* sect. *Raveta* Gideon F.Sm. (Smith 2022a, b). In contrast, *K. sexangularis* is a completely glabrous species that lacks a waxy substance on its leaves. *Kalanchoe xestrelae*, too, is completely non-waxy, with this character not having been observed in first generation plants of the nothospecies. When  $F_2$  hybrids are produced between  $F_1$  generations of *K. xestrelae*, plants could show a very faint waxy layer, but only in some plants, with the vast majority being completely devoid of the leaf wax.

Like both parents, plants of *Kalanchoe xestrelae* generally have an overall light green glaucous to bright red colour (Figure 1). The intensity of the red colouration is more obviously expressed in some forms of the hybrid, but all plants tend to have a significant red infusion. Especially where purplish red-leaved material of *K. luciae*, which is available in the horticultural trade under the moniker ‘Red Lobster’ (Figure 2), was used in creating *K. xestrelae*, the result is a fantastically bright red-leaved form, which is here described as the cultivar *K. xestrelae* ‘Fire Engine’ (Figure 8). This cultivar is slightly smaller-growing than the large, purplish red-leaved variant, so making it a useful groundcover of medium height. In contrast, the purplish red variant of the nothospecies shows significant heterosis, with plants, when in flower, easily reaching a height of about 2.5 m.

***Kalanchoe* ×*estrelae*** Gideon F.Sm. ‘**Fire Engine**’ Gideon F.Sm. **cult. nov.**

**Nomenclatural standard:**—SOUTH AFRICA. Gauteng province.—2528 (Pretoria): Tshwane, (–CA), ex hort., G.F. Smith 1193 (Herb. PRU).

**Description.**—Medium-sized to large, completely glabrous, sparsely branched, multi-annual or perennial shrubs, 0.5–1.0 m tall. Stem erect at first, then leaning. Leaves opposite-decussately clustered along stem or branches, bright red. Other characters as for *K. ×estrelae*.

**Eponymy of cultivar name.**—Plants, especially the leaves, are bright, fire engine-red when grown in full sun.

In general growth form and leaf morphology, material of *Kalanchoe* ×*estrelae* is more reminiscent of *K. luciae* than of *K. sexangularis*. For example, the leaves of *K. ×estrelae* tend to have the shape, but do not always attain the size, of the soup-plate-leaves of *K. luciae*, but the leaf marginal architecture of *K. ×estrelae* varies somewhat from perfectly round (as in *K. luciae*) to shallowly scalloped (as in *K. sexangularis*). Vegetatively, F<sub>2</sub> plants of *K. ×estrelae* tend to develop longer stems, with this character derived from *K. sexangularis*. The desirable low-growing, pseudo-rosulate appearance found in the F<sub>1</sub> generation of the hybrid therefore becomes less pronounced when material of *K. ×estrelae* is inbred.

The inflorescences and flowers of *Kalanchoe* ×*estrelae* are very much intermediate between those of *K. luciae* and *K. sexangularis*. Its inflorescences are not as club-shaped as in *K. luciae*, rather, they can perhaps best be described as a diffusely club-shaped thyrses, with the branches erect to slanted away from the main flowering stem at an angle of 45° (Figure 9). In contrast, the inflorescences of *K. sexangularis* are generally quite diffuse. The flowers of *K. ×estrelae* have a light yellowish green, tubular-urn-shaped corolla tube, with the colour resembling that of *K. luciae* (when the waxy layer is removed) and the corolla lobes are white, also as in *K. luciae*. However, the shape of the corolla lobes is reminiscent of those of *K. sexangularis* (Figure 10). As is often the case with hybrid kalanchoes, the number of floral parts in a whorl can sometimes deviate from the norm of four, with pentamerous flowers being not uncommon (Figure 11).



FIGURE 9.—The corolla tube of *Kalanchoe* ×*estrelae* is light yellowish green while the corolla lobes are white. Photograph: G.F. Smith.



FIGURE 10.—The flowers of *Kalanchoe luciae* are usually densely white-wax-covered (flower on the left). Where the wax was removed from the tube (flower second from the left), the shiny, greenish yellow colour is exposed. The corolla lobes of this form of *K. luciae* are bright white. The slightly curved corolla tube of *K. sexangularis* (flower on the right) is yellowish green with bright yellow corolla lobes. Colour-wise, the tubular-urn-shaped, indistinctly 4-angled, corolla tube of *K. xestrelae* (flower second from the right) as well as the corolla lobes are more reminiscent of those of *K. luciae*. However, the flowers of *K. xestrelae*, which are often also slightly curved, more closely resemble those of *K. sexangularis* in terms of shape. Photograph: G.F. Smith.

Regardless of whether done on a large scale or only for growing a few specimens, propagating *Kalanchoe xestrelae* by stem cuttings or by sowing seed is very easy and rewarding. Although cuttings root more rapidly at the beginning of the growing season in spring, cuttings can be taken at any time of year. With a pair of sharp secateurs, remove short sections – about 100 mm long – of leafy kalanchoe branches and leave the cuttings in the shade for a few days to allow the wounds to dry. The cut ends of the stems can be dipped in root hormone powder, but this is hardly necessary. Afterwards the cuttings can be planted directly in the spot where they are intended to grow, in open beds or in containers.

In general, seed of kalanchoes are very fine and dust-like and usually produced copiously, even in gardens. Freshly harvested seed of *Kalanchoe xestrelae* can be broadcast onto the soil where plants are desired, for example in a rockery or as part of a mixed border. This works best at the beginning of the rainy season. Within 10 to 14 days the first seedlings will appear and eventually it will be necessary to thin them out if the seed germinated too densely.

For more controlled seed propagation and germination, seed can be sown onto the soil in a seedling tray. Ideally the seed should be sprinkled as evenly as possible on the soil surface and the tray at first watered from the bottom by placing it in a larger container filled with water. This will prevent the seedlings, which early on have very flimsy root systems, from being splashed out of the soil when trays are watered from above.

A very thin layer of sand can be sifted onto the seed and small pebbles spread on top of the soil. However, it is not really necessary to cover the seed with a layer of soil – if

the seed is buried deeply in the soil, germination may not take place at all, or at best will be retarded. A loose layer of pebbles assist with supporting the emerging seedlings. The first seedlings will soon appear and once the seedlings have four or more pairs of leaves they can be pricked out and planted directly in the spot where plants are intended to grow, either in open beds, or in containers.

*Kalanchoe ×estrelae* was named for Prof. Dr Estrela Paula das Neves Figueiredo (1963–) of the Ria Olivier Herbarium, Department of Botany, Nelson Mandela University, Gqeberha, South Africa. Estrela has a long-standing interest in succulent plants and, apart from having authored several dozen works on *Kalanchoe* alone, including co-authoring a book on the genus in southern Africa (Smith et al. 2019), is also one of the top ten researchers on the monocot genus *Aloe* globally (Adetunji et al. 2022). It is fitting that this volume of *Flowering Plants of Africa* is respectfully dedicated to her in recognition of her numerous and varied contributions to plant diversity studies in southern and continental Africa.



FIGURE 11.—The aberrant flower of *Kalanchoe ×estrelae* in the centre is pentamerous, rather than tetramerous as in the case of the vast majority of *Kalanchoe* species, including in *K. luciae* and *K. sexangularis*, its parents. Photograph: G.F. Smith.

**Description.**—Biennial to short-lived perennial, few- to many-leaved, unbranched at first, later sprouting from the base, glabrous, medium-sized to robust succulent, 0.6–1.2(–2.5) m tall when in flower. *Stems* reddish green to deep wine-red, unbranched or with few branches, arising from a sturdy base, erect, often with a few lengthwise running ridges, somewhat 4-angled on sterile and fertile shoots. *Leaves* opposite-decussate, green infused with red to a near-uniform deep crimson red to maroon to purple, succulent, spreading to erectly spreading, not longitudinally recurved, coriaceous and papery-flimsy on drying; petiole absent, leaves not clasping the stem; blade 110–150 × 70–80 mm, broadly elliptic or obovate to oblong, often lengthwise somewhat folded upwards, flat to curved up along the margins; base cuneate to narrowly triangular; apex rounded-obtuse; margins smooth or coarsely crenate or undulate-crenate into rounded, harmless, crenations, slightly saucer-like curved upwards. *Inflorescence* a diffusely club-shaped thyrses consisting of several dichasia terminating in monochasia, 500–800 mm tall, erect, apically dense, many-flowered, rather ellipsoid in outline when viewed from above, branches opposite, sometimes only one at a node, erect to slanted away from the main flowering stem at an angle of 45°, subtended by leaf-like bracts, sometimes with leafy branchlets in axils, axis reddish green to bright crimson red; pedicels 4–11 mm long, slender. *Flowers* spreading-erect at anthesis; calyx consisting of 4 sepals; sepals ± 6 × 2.0–2.5 mm, shiny bright green, triangular-lanceolate, succulent, ± separate above, basally fused for ± 1 mm, acute, hardly contrasting against light yellowish green corolla tube; corolla ± 16 mm long, enlarged lower down, tapering to the mouth, not twisted apically after anthesis; tube ± 15 mm long, light yellowish green, tubular-urn-shaped, indistinctly 4-angled, round when viewed from below, longitudinally

indistinctly fluted above; lobes  $5 \times 4$  mm, white infused with light yellowish green, ovate-rectangular, straight lower down, rounded at apex, apiculate. *Stamens* 8, inserted in two ranks, one rank just above the middle of the tube, the other well above the middle of the corolla tube, 4 slightly exserted, 4 included but visible at the mouth; filaments 4–5 mm long, thin, yellow; anthers 0.75–1.00 mm long, yellowish. *Pistil* consisting of 4 carpels; carpels 10 mm long, light green; styles 4 mm long; stigmas very slightly capitate, whitish yellow; scales  $\pm 2$  mm long,  $\pm 1$  mm broad at widest point, tapering towards the apex, tooth-like rounded apically, uniformly light greenish yellow. *Follicles* 6–7(–10) mm long, enveloped in dry, papery, creamy white remains of corolla tube and dry, light brown corolla lobes, drying dull light green, grass spikelet-like, remaining connivent, styles persistent for a long time, calyx drying dull green and diverging from follicles. *Seeds* 0.60–0.75 mm long, light brown, longitudinally obscurely striated with lighter brown, cylindrical to slightly banana-shaped-curved. *Chromosome number*: unknown. Plate 2390.

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*Tephrosia monticola*

Fabaceae

South Africa, Eswatini

***Tephrosia monticola*** K.Balkwill sp. nov. is distinguished from *T. chimanimaniana* Brummitt by its shorter apiculae on the leaflets (0.5–0.8 mm long versus 1.5–2.2 mm long), its narrowly elliptical (rather than subrotund) and narrower (1.5–2.0 mm wide versus 5.1–8.6 mm wide) bracts, its shorter calyx lobes (2–3 mm long versus 5.5–8.3 mm long) and shorter hairs on the calyx lobes (0.5–1.0 mm long versus 1.5–2.2 mm long).

TYPE.—SOUTH AFRICA, Mpumalanga: Louw's Creek, rocky ridge above Ugutugulu Gorge and Shiyalongubu Dam (2531CD), 5 March 2022, *Balkwill et al.* 14536 (J, holotype; K, LYD, MO, PRE, isotypes).

The Leguminosae have been recognised as a natural group of plants since long before the rules of botanical nomenclature were conceived and so their traditional name has been sanctioned by long usage (Turland et al. 2018). The name Fabaceae is a modern equivalent, which is considered equally correct. Members of the family are economically important for crops (for example beans [*Phaseolus vulgaris* L.], peas [*Lathyrus oleraceus* Lam.] and lentils [*Vicia lens* (L.) Coss. & Germ.]), horticulture (for example lupins [*Lupinus polyphyllus* Lindl.] and jade vine [*Strongylodon macrobotrys* A.Gray]), timber (for example kiaat [*Pterocarpus angolensis* DC.] and African blackwood [*Dalbergia melanoxylon* Guill. & Perr.]) and medicines (rooibos tea [*Aspalathus linearis* (Burm.f.) R.Dahlgren] and lucerne [*Medicago sativa* L.]). The family was traditionally considered to comprise three subfamilies, Papilionoideae, Caesalpinioideae and Mimosoideae, but modern systematic investigations using DNA sequences have found that the Mimosoideae are nested within Caesalpinioideae and recognising the Mimosoideae would make the Caesalpinioideae paraphyletic (Käss & Wink 1996; LPWG 2017). Four additional subfamilies have been described (LPWG 2017) and the former Mimosoideae are currently referred to as the Mimosoid clade (LPWG 2017; Souza et al. 2022). The Leguminosae are the third largest family of plants, with about 770 genera and about 19 500 species (LPWG 2017). The Papilionoideae is the largest subfamily in Leguminosae, with 503 genera and 14 000 species (LPWG 2017), and is generally characterised by bilaterally symmetrical flowers with highly differentiated petals known as the standard, wings and keel (Heywood et al. 2007). *Tephrosia* belongs to the tribe Tephrosieae, along with *Millettia* Wight & Arn., *Craibia* Harms & Dunn and *Philenoptera* Hochst. ex A.Rich. (Geesink 1981; Germishuizen 2000).

Members of the genus *Tephrosia* Pers. were described by Linnaeus (1753) under the name *Cracca* L. The name *Tephrosia*, which has been conserved, was published in 1807 by Persoon (1807) and the genus includes approximately 400 species, most of which occur in Africa and Australia with just over 50 species in southern Africa (Germishuizen 2000). Most species are herbaceous or shrubby, although at least six species attain a height of 3 m or more (Coates-Palgrave 2002; Burrows et al. 2018). The parallel veins raised on the



PLATE 2391 *Tephrosia monticola*



lower side of the leaflets makes the species of *Tephrosia* stand out from those of most other genera. A combination of usually setaceous stipules, racemose inflorescences, campanulate calyx tube, clawed standard, which is usually velvety on the adaxial surface, fused filaments, uniform anthers, and linear or ovate compressed two-valved pod with the valves that twist spirally on opening also helps to differentiate the genus from others. *Tephrosia* is divided into two subgenera, of which subgenus *Barbistyla* Brummitt is characterised by having larger flowers (usually longer than 14 mm), forwardly directed wings and keel, standard straight (not first folded over the keel and then reflexed) and a pubescent style. Subgenus *Tephrosia* is more difficult to circumscribe and in view of the related segregate genera, is likely polyphyletic (Kabongo et al. 2017).

Contributions to the knowledge of *Tephrosia* in South Africa include Harvey's (1894) account in *Flora capensis*, in which he nominated 21 species in two sections. In 1948, H.M.L. Forbes published a revision of *Tephrosia* and recognised 67 species (19 of which she described), one with four varieties, one with three and one with two, and she described two new varieties. She organised the species into four sections, which she numbered rather than named. Subsequently, nine of the species she described have been subsumed into synonymy (Nkonki et al. 2003). She also mentioned the extent to which members of the genus had been used as fish poisons, which appeared to operate by stupefying rather than killing fish, and as insecticides. In 1985, Schrire transferred *Mundulea pondoensis* Codd to *Tephrosia*, thus adding the first tree to the genus in South Africa. Two years later, Schrire (1987) published a synopsis of the southern African members of the subgenus *Barbistyla*, in which he reduced two of Forbes' species to subspecies, reduced some tropical species to synonymy and described one new species, *T. brummittii* Schrire.

*Tephrosia monticola* has large flowers (at least 20 × 20 mm) with forwardly directed wings and keel, a straight standard and a pubescent style and so fits comfortably in the subgenus *Barbistyla*. It is most similar to *T. chimanimaniana*, sharing the woody, shrubby or arborescent habit, triangular stipules, leaflets that are held in a 'louvre window' pattern, leaflets that are sericeous below and large attractive flowers. *Tephrosia monticola* differs from *T. chimanimaniana* by the length of the apiculae on the leaflets (0.5–0.8 mm long versus 1.5–2.2 mm long), bract shape (narrowly elliptical versus subrotund), bract width (1.5–2.0 mm wide versus 5.1–8.6 mm wide), length of calyx lobes (2–3 mm long versus 5.5–8.3 mm long) and length of hairs on the calyx lobes (0.5–1.0 mm long versus 1.5–2.2 mm long). The fruit shape, indumentum and the habit of *T. monticola* are very similar to those of *T. praecana* Brummitt, but the leaflets are shorter (up to 25 mm long versus more than 30 mm long), the indumentum on the lower surface of the leaflets is dense rather than sparse, the bracts are narrowly elliptic and acute rather than subrotund with broadly truncate shoulders before having an acute tip, and the indumentum on the calyx includes wispy hairs up to 1 mm long, as well as the dense short hairs that also occur on *T. praecana*. In Schrire's (1987) key, *T. monticola* comes to *T. aequilata* Baker subsp. *australis* Brummitt or to *T. shiluanensis* Schinz. It differs from *T. aequilata* subsp. *australis* by denser, shorter (up to 1 mm long versus up to 1.2 mm long) grey rather than rusty hairs on the rachises and leaflets, shorter (up to 0.7 mm long versus > 1 mm long) hairs on the fruit, and longer (> 55 mm long versus up to 40 mm long) fruits. *Tephrosia monticola* differs from *T. shiluanensis* by the much more robust habit (shrub to tree versus suffrutex), more numerous (5–10 pairs versus 3–6 pairs) leaflets, usually elliptic leaflets with rounded tips rather than

often obovate leaflets with a notched tip, shorter (up to 25 mm long versus > 30 mm long) inflorescence stalk below the first flower, velvety rather than sparsely long pilose calyces, and longer (> 55 mm long versus up to 45 mm long) densely hairy rather than glabrous fruits. *Tephrosia pondoensis* (Codd) Schrire shares the shrub to small tree habit of *T. monticola*, but it has fewer (3 or 4 pairs versus 5–10 pairs) leaflets that are glabrous rather than densely hairy below and orange (versus magenta) flowers. The styles of *T. pondoensis* are glabrous (Schrire 1991).

*Tephrosia monticola* was first collected by Maré Stalmans on the farm Vooruitzicht 374JU in the Panhandle area of Songimvelo Game Reserve in February 1994. It has subsequently been collected in Eswatini by Linda Loffler in April 2001 (*Loffler sub Dobson-Loffler Herbarium* 464). The next collection dates were from April 2005, when it was collected by John Burrows and Mervyn Lötter on a Mpumalanga Plant Specialist Group (PSG) outing to Mandendeka Mountain on the edge of the Satco Plantations. The species was collected again in March 2022 on a hillside above Shiyalongubu Dam and Ugutugulu Gorge on a Mpumalanga PSG outing (Figure 1a). The specimens at this site were mainly between one and two metres tall, so two of us (KB and DO) returned to the Mandendeka locality in April 2022 to find one plant of four metres tall (Figure 1b), along with the three-metre-tall plants that had been reported (Figure 1c), thus firmly establishing *T. monticola* as another tree species in the genus in South Africa. The stems of the larger specimens were between 65 mm (Figure 2a) and 105 mm in diameter near their bases.

Most species of *Tephrosia* are shrubs or herbs, but several species that reach three or more metres tall, and thus qualify as trees, occur along the mountains of southern Africa. These include *T. aequilata*, which occurs from Limpopo through to Kenya, *T. montana* Brummitt, which occurs in Zimbabwe and Mozambique, *T. noctiflora* Bojer ex Baker, which occurs from South Africa to Kenya and also in West Africa, *T. praecana*, which occurs in Zimbabwe and Mozambique, and *T. vogelii* Hook.f., which is widely cultivated and possibly indigenous in Mozambique (Burrows et al. 2018). In addition, *T. pondoensis*, which occurs in Eastern Cape and KwaZulu-Natal, has been recorded as reaching five metres (Schrire 1985). *Tephrosia monticola* brings the total number of trees in the genus in Africa to seven and the number in South Africa to four, although *T. aequilata* and *T. noctiflora* have not been recorded as trees in South Africa (Nkonki et al. 2003).

All known specimens of *Tephrosia monticola* have been collected in the mountains near the South Africa–Eswatini border, between Jeppes Reef and Forbes Reef (Figure 3). The species should be added to the list of endemics of the Limpopo–Mpumalanga–Eswatini Escarpment (Clark et al. 2022). All sites at which *T. monticola* have been recorded so far are between 1 020 m (*Balkwill & Oosthuizen* 14565) and 1 600 m (*Loffler sub Dobson-Loffler Herbarium* 464) above sea level. *Tephrosia monticola* has been recorded in open woodland or lightly wooded grassland among rocks on steep rocky slopes or on cliff edges, all within Barberton Montane Grassland Gm17 (Mucina & Rutherford 2006). All localities are on the quartzose metasandstones of the Moodies Group (Ward 2000). The northernmost collection is from Mandendeka. Other than Kaalrug (highest point 891 m) and the adjacent Big Buffalo (highest point 938 m), all the area to the north and west of Mandendeka is either planted to timber or is lower than 1 000 m altitude. Although Big Buffalo is of the correct geological formation, it is unlikely that *T. monticola* will grow at an altitude as low as



FIGURE 1.—*Tephrosia monticola* in habitat: a, habitat at type locality above Ugutugulu Gorge; b, 4 m tall tree (light green leaves) at Mandendeka overshadowed by an escaped *Eucalyptus* tree (scale – K. Balkwill standing level with tree base and 1.75 m tall); c, about 3 m tall tree at Mandendeka (scale – K. Balkwill standing slightly below base of tree and 1.75 m tall). Photographs: a, K. Balkwill; b, c, D. Oosthuizen.

937 m. Forbes Reef is near the southern limit of the Moodies Group, so it is unlikely that *T. monticola* will be found further south than the Loffler collection from near Malolotja Falls (*Loffler sub Dobson-Loffler Herbarium* 1291). A polygon linking the current known collection points on Google Earth provides an area of 416 km<sup>2</sup>. The Moodies Group does extend beyond this area, so a maximum Extent of Occupancy (EOO) is likely 600 km<sup>2</sup>. Area of Occupancy (AOO), because of the very specific habitat, both in terms of geology and rocky outcrops will be much less and probably in the region of 100 km<sup>2</sup> at maximum.



FIGURE 2.—*Tephrosia monticola* characters: a, bark of a mature tree at Mandendeka; b, style and free portion of stamens usually covered by tip of keel at Mandendeka; c, bark on branchlet with lenticels at Ugutugulu; d, damaged area on branchlet demonstrating how thick the bark is. Photographs: a, b, D. Oosthuizen; c, d, K. Balkwill.

The number of plants at Mandendeka is in the region of 60 individuals, at Ugutugulu in the region of 30 individuals and 10 individuals at Malolotja Falls, which suggests that the maximum total number of individuals will definitely be less than 10 000 and possibly less than 2 500. Some of the suitable area has been planted to *Eucalyptus* L'Hér. and may have caused a historical reduction of about 20% of the population. *Eucalyptus* is escaping into the undisturbed area (Figure 1b) together with *Acacia mearnsii* De Wild. and these represent threats to *T. monticola*. The assumed historical loss of individuals due to afforestation

is less than the thresholds for Criterion A (IUCN 2012). Although the EOO and AOO fulfil the criteria for Endangered under Criterion B and although there are currently fewer than 10 locations known (Criterion B2a), *T. monticola* does not fulfil Criteria B2b or B2c. Under criterion C, *T. monticola* fulfils the criterion for the number of mature individuals, but it does not fulfil the criteria for decline (i.e., Criterion C1 or C2). Under Criterion D, it is not likely (although possible) that the number of individuals is less than 1 000. No quantitative analysis has been done to facilitate application of Criterion E. Three of the six known localities are in proclaimed nature reserves. Thus, a provisional threat status of Least Concern is suggested.

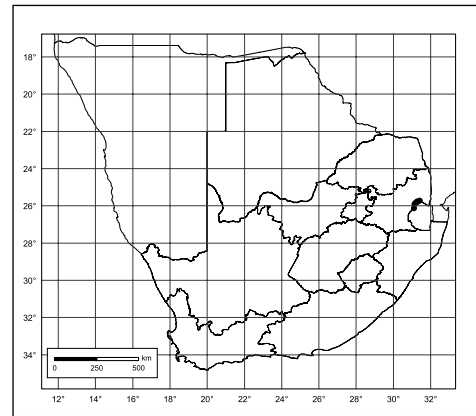


FIGURE 3.—Distribution of *Tephrosia monticola* in southern Africa, based on herbarium collections.

Specimens have been collected in flower between March and April, but some plants already had fruits in February, indicating that flowering must have started earlier. Flowering is then likely to be from January to April and fruiting from February through to May. Flowers of *T. monticola* are magenta and have contrasting nectar guides (darker veins and a very light greenish cream triangle on the standard). The flowers are strongly zygomorphic and the sexual parts are hidden and require the keel to be moved down in order for them to make contact with a pollinator. A large proportion of the upper proximal area of the outer surface of the wings has sculpturing that would provide grip for a pollinator to force its head under the standard and hence push the keel downwards. The disc, which looks like a miniature calyx inside the base of the staminal tube, will produce nectar (Moore 1936) and the callosities on the adaxial stamen and the upper edge of the staminal tube will function to restrict access to the nectar (Westerkamp 1999). All of these features and the size of the flowers suggest that they are pollinated by largish solitary bees. Flowers in a plant press two days after collection had a very sweet scent. If living flowers also have a sweet scent, this could also play a role in attracting bee pollinators.

The flowers are large and attractive and the compact, shrubby growth form of this *Tephrosia* make it a potential candidate for horticulture. Seeds were successfully germinated at Whyte Thorne Botanical Garden where seedlings were planted out and grew to 2 m tall. Surrounding trees grew faster and shaded the saplings and they died, suggesting that this species needs to be grown in the sun.

The generic name *Tephrosia* refers to the ashy colour of the leaves, which is imparted by the greyish indumentum on many species (Quattrocchi 2000). The specific epithet, *monticola*, means living in the mountains. As yet, there is no known common name for this species.

### Additional specimens examined

ESWATINI. **2531** (Komatipoort): near Bulembu Mountain, Devil's Bridge, 1600 m (–CC), 29 April 2001, *Loffler sub Dobson-Loffler Herbarium 464* (Dobson-Loffler Herbarium). **2631** (Mbabane): Malolotja Nature Reserve, Near Malolotja Falls, 1284 m (–AA), 14 May 2022, *Loffler sub Dobson-Loffler Herbarium 1291* (Dobson-Loffler Herbarium).

SOUTH AFRICA, Mpumalanga: **2531** (Komatipoort): Barberton District, on the farm Kamslubanakop 268JU, 1105 m (–CB), 21 December 2004, *Lötter 1042* (LYD, PRE); southeast of Louw's Creek, Kamhlabane, SATICO Forestry, their most SE corner (–CB), 17 April 2005, *McMurtry 12542* (HSMC, PRE); Barberton Mountains, Satico Plantation, Mandendeka, 1090 m (–CB), 17 April 2005, *Burrows & Lötter 8942* (BNRH now at J, LYD); Barberton Mountains, Satico Plantation, Mandendeka, 1020 m (–CB), 28 April 2022, *Balkwill & Oosthuizen 14565* (J, K, MO); Songimvelo Game Reserve, on the farm Vooruitzicht 374JU, 1200 (–CC), 28 February 1994, *Stalmans 2923* (J, LYD); East of Barberton, East of Twello, South of Shiyalongubu Dam, in Ugutugulu River Gorge (–CD), 8 September 2002, *McMurtry 10700* (HSMC).

**Description.**—Perennial woody shrub, single- or multi-stemmed from base, usually more than 1 m tall and sometimes a small tree to 4 m tall and with base up to 105 mm in diameter; young stems ribbed, densely pubescent with ascending grey hairs; branchlets with short internodes 3–5 mm long and thick, brown, markedly lenticellate bark; main stem with corky and scaly bark, old bark dark brown or grey below scales, tan where new bark fills fissures. Leaves with 5–10 pairs of opposite lateral leaflets and a terminal leaflet; rachis 25–45 mm long (excluding petiole), prolonged about 2 mm beyond upper pair of lateral leaflets, densely pubescent with appressed and ascending grey hairs about 1 mm long, petiolules about 2 mm long, densely pubescent; leaflets narrowly elliptic, oblong or slightly obovate, 13–23 × 5–8 mm, rounded with 0.5–0.8 mm apiculus, rounded at base, bright green and glabrous above, darker green and with dense greyish appressed hairs below; midvein especially prominent below, secondary veins raised to slightly raised below; petiole 4–7 mm long. *Stipules* ovate to triangular, 2.5–3.0 × 2.0–2.5 mm, light brown and pubescent without, dark reddish brown, shiny and glabrous within. *Inflorescence* racemose, on stalk up to 25 mm long and inflorescence up to 40 mm long (excluding stalk) with up to 20 flowers; bracts elliptic, about 8 × 1.5–2.0 mm, densely puberulous with light greyish hairs up to 1 mm long, reddish brown, caducous; pedicels about 6.5 mm long at flowering and about 9 mm long in fruit. *Calyx* cupular, reddish brown to light green, with spreading greyish hairs up to 1 mm long without, glabrous within; tube about 4 mm deep and 4 mm wide; weakly bilabiate with upper lobes about 3 × 2 mm and united for 2 mm of their length and with lower lobes triangular, 2 × 2 mm. *Corolla* with standard almost square with broadly rounded corners, about 20 × 20 mm, lilac or light magenta with fine magenta linear nectar guides leading to a light greenish cream triangle at the base, densely sericeous with reddish brown hairs up to 0.7 mm long on the outer surface, with many veins radiating from the base, base broadly cuneate, 5 × 2.5 mm at the bottom and 6 mm wide at the top, with adaxially protruding folds at the junction of blade and claw; wings obliquely obovate, 20 × 8.5 mm at widest point and 4 mm wide at the base, dark magenta fading to white near the base and the lower section of the midrib, tip rounded, markedly sculptured along upper side for  $\frac{2}{3}$  of length and  $\frac{2}{3}$  of width, base truncate and rounded on upper side, cuneate on lower side, claw 4 × 1.5 mm, adhering to base of keel by means of folding; keel glabrous, with minute multicellular globose or curved and pointed swellings along suture, dark magenta at tip, magenta along the upper edge, fading to white on lower edge, blades joined on lower edge for distal half, almost semi-circular in profile, 17 × 10 mm at widest point and 4 mm wide at base,

flattened over stamens, lower edge in line with margin of claw, upper edge of base truncate and rounded, tip slightly narrowed and rounded, claw  $4 \times 1.5$  mm. *Stamens* with filaments united into a tube, inflected upward at 18 mm from base, white, upper filament free for lower 7 mm, with callosity 2 mm from base, other 9 filaments fused from base, with callosities 2 mm above base on upper edge of tube, all filaments free from 18 mm from base at point of inflection, free portion of inner filaments 3.5 mm long and outer filaments 6 mm long, so that there are two rings of anthers, one 2.5 mm above the other; anthers all basifixed, elliptic,  $1.2 \times 0.5$  mm, bright yellow; pollen globose, cream-coloured. *Disc* cupular, sub-bilabiate, upper lip 1 mm long, with 2 minute teeth, lower lip 2.5 mm long, with 3 minute teeth. *Gynoecium* with ovary cylindrical, tapering to tip,  $16 \times 1.5$  mm, with 8 ovules, densely appressed sericeous; style curved upwards at tip of ovary, 7.5 mm long, dorsoventrally flattened, about  $1 \times 0.5$  mm at base, tapering to  $0.7 \times 0.5$  mm halfway along its length, widening to  $0.9 \times 0.5$  mm near tip and then tapering towards stigma, with patent hairs about 0.5 mm long in upper  $\frac{3}{4}$ ; stigma globose, about 0.3 mm in diameter, with minute tentacular receptive scales. *Pod* linear, slightly upturned near tip,  $55\text{--}75 \times 6.5\text{--}8.0$  mm, with thickened rims, velvety pubescent with greyish hairs to 0.7 mm long, valves twisting into a spiral on opening. *Seeds* oblong,  $7 \times 3.5\text{--}4.0 \times 2.5$  mm, brown with creamy remains of pulp on surface, hilum more or less central on upper edge, narrowly oval, surrounded by rim formed by funicle. *Flowering time*: January to April. *Fruiting time*: February to May. Plate 2391.

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PLATE 2392 *Ophrestia oblongifolia* var. *oblongifolia*

*Ophrestia oblongifolia* var. *oblongifolia*

Leguminosae: Papilionoideae

South Africa, Eswatini

***Ophrestia oblongifolia*** (E.Mey.) H.M.L.Forbes var. ***oblongifolia*** in Bothalia 4: 1004 (1948). *Cracca oblongifolia* Kuntze: 175 (1891). *Glycine wilmsii* Harms: 302 (1899). *Ophrestia nervosa* H.M.L.Forbes: 1006 (1948). *Ophrestia retusa* H.M.L.Forbes: 1005 (1948). *Ophrestia swazica* H.M.L.Forbes: 1005 (1948).

*Ophrestia oblongifolia* var. *oblongifolia* is a member of the family Leguminosae, subfamily Papilionoideae (Verdcourt 1970). It is classified in the tribe Phaseoleae (Fabaceae), subtribe Ophrestiinae, which includes two other genera along with *Ophrestia* H.M.L.Forbes: the tropical African *Pseudoeriosema* Hauman and the Southeast Asian *Cruddasia* Prain (Lackey 1977).

There have been various attempts to construct a phylogeny of the tribe Phaseoleae, but there are conflicting views on the relationships between Ophrestiinae and the other subtribes (Kajita et al. 2001; Hu et al. 2002; Wojciechowski et al. 2004; Schrire 2005). However, the molecular datasets used only included two African *Ophrestia* species, which were placed within a larger Millettieae clade (Kajita et al. 2001), and thus phylogenetic studies on the subtribe are still preliminary (Schrire 2005; Moteetee & Van Wyk 2012).

Lackey (1977) believed that the Ophrestiinae originated in Asia. However, only three of the 16 species in *Ophrestia* are from Asia. The highest abundance of *Ophrestia* species is in tropical Africa (eight species) with four species known from Madagascar, and only one in southern Africa – *O. oblongifolia*. While the centre of diversity is thus African, it is conceivable that the origins of the subtribe could be Asian, but confirmation of this must await a well-sampled phylogeny and biogeographic analysis.

*Ophrestia oblongifolia* was originally described by Meyer (1836) as a member of the genus *Tephrosia* Pers., with the epithet of *oblongifolia* due to its oblong leaflets. Forbes (1948) argued that *T. oblongifolia* was the only species that did not have the typical *Tephrosia* characteristic of close parallel veining of the leaflets fusing with the margin, but rather 5–7 widely spaced lateral veins that loop back without fusing with the margin. A new genus was thus created for this species and given the name *Ophrestia*, an anagram of *Tephrosia*. Three other species were also included in this genus: *O. nervosa*, *O. retusa* and *O. swazica* (Forbes 1948). In addition, Forbes (1948) attributed Harms' holotype specimen of *Glycine wilmsii* (Wilms 383), under the species *Ophrestia nervosa*, but also cited the name as a synonym for *O. oblongifolia* with the words 'in part'. This particular specimen (from Lydenburg, South Africa) had been described in 1899 by Harms as *Glycine wilmsii*. This ambiguous treatment of the name as a synonym is therefore contentious, as highlighted by Verdcourt

(1970), who placed *O. nervosa*, *O. retusa* and *O. swazica* into synonymy with *O. oblongifolia* var. *oblongifolia*. He claimed that the leaf characters Forbes used to distinguish these three species were too variable and impractical, which therefore led to the new and current description of *O. oblongifolia* var. *oblongifolia*. It is also interesting to note that Harms thought the classification of the species into *Glycine* Willd. was questionable because of the leaflet characteristics that did not correspond to other species in *Glycine*.

Further genus level changes were enacted by Hermann (1962) who created *Paraglycine* F.J.Herm. and *Pseudoglycine* F.J.Herm. for extraneous species of *Glycine*, recognising the similarity of these two new genera to *Ophrestia*. Verdcourt (1970), however, combined the genera *Paraglycine* and *Pseudoglycine* with *Ophrestia*, as he deemed the characters given by Hermann (1962) to be inadequate to separate them. Verdcourt (1970) also thought *Glycine* to be allied to *Ophrestia*. However, Lackey (1977) described this association as a result of superficial resemblance and argued that there is no relation between the two genera, since *Glycine* has ternate leaves, whilst *Ophrestia* has 1–5-jugate leaves. Moreover, *Ophrestia* has shorter petioles, silkier petals and protruding seed arils, whereas *Glycine* has glabrous petals, and seeds lacking an aril (Lackey 1977, 1981).

In the most recent taxonomic treatment, *Ophrestia oblongifolia* was lectotypified by Moteetee & Van Wyk (2012). The specimen selected as the lectotype was an unnumbered specimen collected by Drège, kept in the Paris Herbarium (P) at the Muséum National d'Histoire Naturelle in France. This was the only specimen with fruits, which are documented in Meyer's (1836) original description, and is also annotated by Meyer.

*Ophrestia oblongifolia* comprises two varieties namely, *O. oblongifolia* var. *oblongifolia* and *O. oblongifolia* var. *velutinos*a H.M.L.Forbes. The former variety is distinguishable by being less robust and having fewer leaflets (3–7 leaflets) when compared to *O. oblongifolia* var. *velutinos*a (3–11 leaflets). Furthermore, in *O. oblongifolia* var. *oblongifolia* whitish hairs are thinly to densely arranged across the whole plant, whereas *O. oblongifolia* var. *velutinos*a has dense brownish hairs (Moteetee & Van Wyk 2012). Verdcourt (1970) deemed *O. oblongifolia* var. *velutinos*a a 'genuine variant', but only to a minor extent. The differences are, indeed quite subtle, which suggests that the taxonomic rank of *O. oblongifolia* below species level could be subjective and thus the recognition of these taxa as varieties may be unwarranted.

As previously mentioned, *Ophrestia oblongifolia* var. *oblongifolia*, along with its companion variety, are the only taxa of the genus that are found in southern Africa, occurring in the South African provinces of Limpopo, Eastern Cape, KwaZulu-Natal, North West, Mpumalanga and Gauteng, and in the Mbabane area in Eswatini (Moteetee & Van Wyk 2012). The distribution of *O. oblongifolia* var. *oblongifolia* is interesting in that there appears to be a disjunction between two main areas of distribution, separated by the Drakensberg and Great Escarpment region (Figure 1). It is unclear if this disjunction is genuine or merely a consequence of a lack of sampling. *Ophrestia oblongifolia* var. *velutinos*a is mostly restricted to the coastal regions of KwaZulu-Natal, where it overlaps with *O. oblongifolia* var. *oblongifolia*.

*Oprestia oblongifolia* var. *oblongifolia* (Figure 2) typically grows along a wide range of altitudes, from almost sea level at the coast to 1 700 metres above sea level. It can be found on moderately sloped grasslands with sandy, stony or rocky soil that varies from approximately 0.1 to 0.8 m in depth (Bezuidenhout et al. 1994; Nkonki 2003). It tends to wither during the winter season and is fire-stimulated, resprouting in mid- to late spring after late winter veld fires, but it will also resprout during this time in the absence of fire. Thereafter, it will grow and flower optimally during early summer in November (A.E. van Wyk, personal communication). This taxon has an IUCN Red List status of Least Concern (Raimondo et al. 2009).

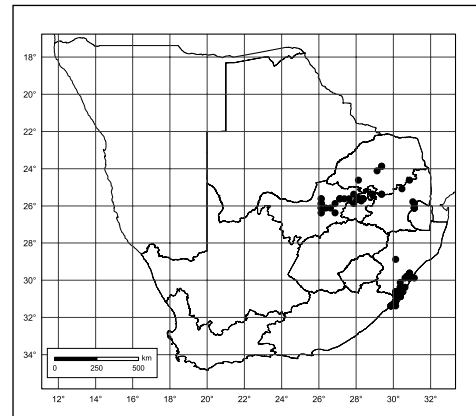


FIGURE 1.—Known geographical distribution of *Oprestia oblongifolia* var. *oblongifolia* in southern Africa.

The uses of this variety have not been documented. However, a study conducted by Mazel (1992) on the Collingham Shelter, located south of the Thukela basin on the outskirts of the Drakensberg in (then) Natal, South Africa, recorded that *Oprestia oblongifolia* was used traditionally by the Natal hunter-gatherers who inhabited the shelter. The authors recovered *O. oblongifolia* assemblages (such as seeds) from a series of excavations of the late Holocene deposits. It was believed that the hunter-gatherers used the species as a source of firewood around 1260 and 650 BP. There have been no additional records of this plant having any other value such as medicinal or economic importance, and there are no listings of it being toxic or edible. There is also a dearth of information on pollination and seed dispersal, and this species has no known common name.

**Description** (based on Moteetee & Van Wyk (2012)).—Scandent herb with creeping or trailing stems from perennial, woody rootstock, up to 1 m wide, 150–300 mm high, thinly pubescent throughout. Leaves 3–7-foliolate, subsessile, rarely unifoliolate; leaflets oblong, 40–75 × 20–30 mm, densely silky beneath with whitish hairs, glabrescent above; petiole (25–)45–80 mm long; stipules linear-lanceolate, 5–7 × 1–2 mm, green on both sides, netted-veined; stipels absent. Inflorescences few- to many-flowered axillary racemes; peduncles 70–350 mm long. Flowers variable in colour, purple, purplish pink, violet, white, whitish pink, yellow or bluish purple, (6–)11–15 mm long, hairy. Bracts persistent, linear-lanceolate, 4–6 × ± 0.5 mm; bracteoles linear-lanceolate, 2–3 × ± 0.2 mm. Calyx bilabiate, densely covered in silky brownish hairs, two upper lobes fused up to two-thirds of their length; upper lip 6–8 mm long; lower lip 6–8 mm long. Petals with standard oblong, 10–12 × 4–6 mm, silky on outside, claw 2–4 mm long; wings oblong, 6–10 × 4–6 mm, silky on outside, claw ± 3 mm long; keel narrowly elliptic, 5–9 × 3–4 mm, claw 3–4 mm long. Stamens diadelphous, vexillary stamen slightly joined to others. Ovary 4–5 mm long, linear-oblong, 2–4-ovuled; style with few hairs along one side, curved upwards. Fruit 20–40 × 7–8 mm, coriaceous, fulvous-hairy, laterally compressed, 1–2-seeded legume. Seeds brown to black, oblong to ovoid, ± 4 × ± 3 mm, aril prominent. Flowering time: November–February. Chromosome number: unknown. Plate 2392.



FIGURE 2.—*Ophrestia oblongifolia* var. *oblongifolia* in habitat: a, inflorescences; b, whole plant showing sprawling habit; c, close up of flower. Photographs: a, A.E. van Wyk and S. Malan; b, S.P. Bester (<https://www.inaturalist.org/photos/167887894>); c, C. Bravard (<https://www.inaturalist.org/observations/82040692>).

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*Vigna vexillata*

Fabaceae: Papilionoideae: Phaseoleae

*Africa; southern Asia; Australia; northern, South and Central America*

***Vigna vexillata*** (L.) A.Rich. in De la Sagra, R., *Historia física, política y natural de la Isla du Cuba* (Spanish ed.) 10: 191 (1845); Bentham: 194, t.50/1 (1859); Harvey: 240 (1862); Baker: 199 (1871); Baker: 413 (1929); Burt Davy: 420 (1932); Wilczek: 379, t. 29 (1954); Hepper: 566 (1958); Verdcourt: 652 (1971); Maréchal et al.: 200 (1978a), 202 (1978b); Pienaar & Kok: 237 (1991); Pasquet: 145 (2001). *Phaseolus vexillatus* L.: 724 (1753). *Dolichos vexillatus* (L.) Kunth: 440 (1824), nom. illeg. *Vigna vexillata* f. *typica* Domin: 225 (1926), nom. inval.

*Vigna vexillata* (L.) A.Rich. is a pantropical species that is morphologically and ecologically diverse, and economically important. It is locally known in southern Africa as *wilde-akkerboontjie*, *wilde-ertjie* (Afrikaans); wild-cowpea, wild sweet pea (English); *mgcenga* (Swati); and *isikhwali*, *ubombo*, *umcwasibe*, *umnxwasibe* (Zulu) (Pooley 1998; Wells et al. 1986). It is characterised by its striking, large whitish to dark pink papilionate flowers with yellow nectar guides, and the peculiar, twisted keel that plays an important role in its ‘hugging’ pollination strategy (Hedström & Thulin 1986; Pienaar & Kok 1991; Delgado-Salinas et al. 2011).

The genus *Vigna* Savi belongs to the large, species-rich and economically important family Fabaceae Lindl. It is the third largest plant family following Orchidaceae Juss. and Asteraceae Bercht. & J.Presl in size, and the second most important globally after the Poaceae (cereals) in view of food production (Smýkal et al. 2015). Members of the Fabaceae, also known by its alternative name Leguminosae Juss. (Lewis et al. 2005), are characterised by their distinct fruit, a legume. The term ‘legume’ is derived from the Latin word *legumen* (Vasconcelos et al. 2020) and consists of a single carpel, with ovules attached to the ventral suture that opens along one or both sutures when dehiscent (Spjut 1994; Harris & Harris 1995).

Fabaceae species are diverse in growth form, ranging from herbs, shrubs, trees and climbers to aquatics. The distribution of this family is regarded as cosmopolitan, as they are absent only from Antarctica (Harris 2004; Karuniawan et al. 2006; Damayanti et al. 2010; Marubodee et al. 2015). Members of the family occur in a wide range of habitats, from dry to seasonally dry tropical forests, thicket and bushland, to tropical wet forests and temperate biomes (Schrire et al. 2005; DRYFLOR 2016; LPWG 2017).

Legumes are used to produce high quality pasture, cover and cash crops, with their seeds being an important source of protein (Vanderborgh 1989). They are also used in soil fertilisation and control of soil erosion (Graham & Vance 2003; Gepts et al. 2005; Lewis et al. 2005; Trytsman et al. 2011) because of their ability to nodulate and fix atmospheric nitrogen in the soil (Trytsman et al. 2011). They also produce high value protein

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PLATE 2393.—Flowering and fruiting stems of *Vigna vexillata* var. *angustifolia* showing the typical linear-lanceolate leaflets with truncate bases, glabrescent stems and leaves, and hirsute fruits with exposed seeds, × 1. Voucher specimen: Condý 312 in National Herbarium (PRE), Pretoria. Artist: Gillian Condý.



PLATE 2393 *Vigna vexillata*



and micronutrients that carry health benefits that are particularly useful in underdeveloped parts of the world (LPWG 2017). Some of the earliest cultivated legumes used as food sources (pulses) include species that belong to tribes Phaseoleae DC., Fabae Rchb., Ciceraceae Alef. and Genisteae Dumort, e.g., soybeans (*Glycine max* (L.) Merr.) and mungbeans (*Vigna radiata* (L.) R.Wilczek) from East Asia; faba beans (*Vicia faba* L.), lentils (*Vicia lens* (L.) Coss. & Germ. = *Lens culinaris* Medik.), chickpeas (*Cicer arietinum* L.) and peas (*Lathyrus oleraceus* Lam. = *Pisum sativum* L.) from the Fertile Crescent of the Middle East; and common beans (*Phaseolus vulgaris* L.) and lupins (*Lupinus polyphyllus* Lindl.) from Central and South America (Smýkal et al. 2015). Other important pulses include species from the bean genus *Phaseolus* L., pigeon peas (*Cajanus cajan* (L.) Huth) and cowpeas (*Vigna unguiculata* (L.) Walp.) (Graham & Vance 2003). Most of the legumes cultivated for pasture in South Africa are introduced and have been extensively beneficial to the South African agricultural sector (Trytsman et al. 2011). Commercially cultivated indigenous legumes include *Aspalathus linearis* (Burm.f) R.Dahlgren (rooibos) from tribe Crotalariae Hutch. and *Cyclopia intermedia* E.Mey. (honey bush) from the Podalyrieae Benth., both found in the Cape Floristic Region and popular for their culinary (tea) and medicinal values (Trytsman et al. 2011).

Tribe Phaseoleae was established in 1825 and forms part of the Papilionoideae DC. subfamily. It has subsequently been treated by Bentham (1837, 1865), Taubert (1894), Hutchinson (1964), Lackey (1977, 1981) and Baudet (1978). However, the tribe's circumscription has been problematic, as it is not monophyletic. Lackey recircumscribed the tribe in 1981, recognising 84 genera and c. 1 480 species (Lackey 1981; Lewis et al. 2005), but since these treatments, several genera have been moved to other tribes, e.g., Millettiae Miquel., Desmodieae (Benth.) Hutch. and Diocleae (Benth.) Hutch. reinstated by De Queiroz et al. (2015). More work is currently ongoing to clarify relationships within the Phaseoleae. One of the genera within Phaseoleae, *Vigna*, has traditionally been thought to comprise some 150–200 species, but *Vigna* s.s. contains 105 species, with 11 species in South Africa (Klopper & Winter 2022). The New World species of *Vigna* has a closer affinity to other New World genera of the subtribe Phaseolinae than to *Vigna* s.s. (Schrire 2005; Delgado-Salinas et al. 2011; Catarino et al. 2021). The genus has a pantropical distribution and occurs in subhumid tropical climates in Africa (Singh et al. 1997; Timko & Singh 2008; Catarino et al. 2021). Verdcourt (1970) recognises eight subgenera within *Vigna*. Four of these subgenera are represented by species in southern Africa: subgenus *Vigna*, subgenus *Plectrotropis* (Schumacher.) Baker, subgenus *Haydonia* (R.Wilczek) Verdc. and subgenus *Catjang* (DC.) Jaaska & Jaaska.

*Vigna vexillata* together with *V. lobatifolia* Baker currently forms part of subgenus *Plectrotropis*. The subgenus name, *Plectrotropis*, is derived from the Greek words *plectro* (meaning 'spur') and *tropis* (meaning 'keel of a ship'), which reflects the characteristic hollow spur located on the left side of the keel (Pienaar & Kok 1991), evident in these two species. *Vigna vexillata* was first described in the second volume of *Hortus Elthamensis*, a pre-Linnaean publication by the British botanist of German descent, Johann Jakob Dillenius (1732), as *Phaseolus flore odorato, vexillo amplo patulo* (translated: 'plant with fragrant flowers, the standard widely spreading') based on material collected in Havana (Dillenius 1732; Stafleu & Cowan 1976). Carolus Linnaeus, the Swedish botanist, redescribed Dillenius' species in his *Species Plantarum* (1753) as *Phaseolus vexillatus* L. based on the plate painted by Dillenius. The iconotype was lectotypified by Verdcourt in 1971 (Jarvis 2007). Achille

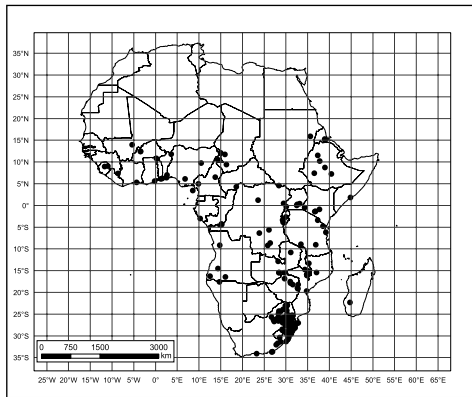


FIGURE 1.—Known distribution range of *Vigna vexillata* in Africa.

Richard moved the species to *Vigna* in 1845, a genus that was already established in 1824 by Savi.

*Vigna vexillata* is a variable taxon with a pantropical distribution. In South Africa, it occurs from Limpopo southwards through Mpumalanga, Gauteng, North West, Free State, KwaZulu-Natal, Eastern Cape and up to Knysna in the Western Cape (Figure 1). Due to its wide distribution, variability is evident in the number of synonyms that exist for different morphs described from across its distribution range. A selection of synonyms (Verdcourt 1970, Pienaar & Kok 1991, LPWG 2021), relevant to South Africa only, are presented here:

1. *Vigna vexillata* var. *angustifolia* (Schumach. & Thonn.) Baker: *Dolichos angustifolius* Vahl ex Guill. & Perr., *Dolichos stenophyllus* Gagnep., *Phaseolus novo-guineensis* Warb., *Plectrotropis angustifolia* Schumach. & Thonn., *Vigna angustifolia* (Schumach. & Thonn.) Hook.f., *Vigna hirta* Hook., *Vigna valetonii* Pulle, *Vigna vexillata* var. *linearis* Craib
2. *Vigna vexillata* var. *davyi* (Bolos) B.J.Pienaar: *Vigna davyi* Bolus
3. *Vigna vexillata* var. *ovata* (E.Mey.) B.J.Pienaar: *Phaseolus capensis* Thunb., *Phaseolus capensis* var. *lanceolata* E.Mey., *Phaseolus capensis* var. *longifolia* E.Mey., *Phaseolus capensis* var. *ovatus* E.Mey., *Strophostyles capensis* (Thunb.) E.Mey.
4. *Vigna vexillata* var. *vexillata*: *Dolichos cylindricus* Desv. ex Ham., *Phaseolus glycinaeformis* Weinm., *Phaseolus humifusus* Savi, *Phaseolus pulniensis* Wight, *Phaseolus sepiarius* Dalzell, *Phaseolus quadriflorus* A.Rich., *Plectrotropis hirsuta* Schumach. & Thonn., *Phaseolus vexillatus* L., *Strophostyles capensis* (Thunb.) E.Mey., *Vigna carinalis* Benth., *Vigna crinita* A.Rich., *Vigna golungensis* Baker, *Vigna hirta* Hook., *Vigna phaseoloides* Baker, *Vigna scabra* Sond., *Vigna senegalensis* A.Chev., *Vigna thonningii* Hook.f., *Vigna tuberosa* A.Rich., *Vigna vexillata* var. *hirta* (Hook.) Baker f., *Vigna vexillata* var. *thonningii* (Hook.f.) Baker, *Vigna wightii* Benth.

Previously, *Vigna davyi* was included in subgenus *Plectrotropis*, but was sunk to varietal level within *V. vexillata* by Pienaar & Kok (1991). The placement and rank of *V. lobatifolia* was also in question in two studies, one using isozyme polymorphisms (Sonnante et al. 1996) and another molecular data (Takahashi et al. 2016). The former study suggested that *V. lobatifolia* should be considered a variety of *V. vexillata* (Sonnante et al. 1996), but Takahashi et al. (2016) pointed out that, although their molecular evidence suggested similar results, they maintained it as an independent species due to its morphological distinctness and unique habitat, occurring in the Namib Desert. Therefore, the taxonomic rank of species level for *V. lobatifolia*, as recognised by Verdcourt (1970) and LPWG (2021), is retained here. *Vigna vexillata* differs from *V. lobatifolia* in its rootstock (fusiform versus moniliform with tuberous swellings), indumentum (ferruginous or setaceous versus pale or white



FIGURE 2.—*Vigna vexillata* var. *vexillata*: a, tripinnate leaf showing the typical ovate leaflets with obtuse bases and twining stems; b, mature seeds; c, flower and two young fruits; d, a close-up of the flower showing the yellowish nectar guides at the base of the standard petal, the twisted keel beak with a spur on the left-hand petal (arrow) and the style with hairy brush protruding from the keel beak apex; e, flowers borne on long peduncles. Photographs: a, e, J. Swart; b, M.M. le Roux; c, d, M. Koekemoer.

ferruginous, velutinous, or setose), leaves (leaflets soft textured and unlobed versus coriaceous and often basally lobed) and fruit (cylindric versus compressed) (Pienaar & Kok 1991).

*Vigna vexillata* (Figure 2) includes a total of nine varieties (LPWG 2021), with four represented in southern Africa, i.e., *V. vexillata* var. *vexillata*, *V. vexillata* var. *angustifolia* (Schumacher & Thonn.) Baker, *V. vexillata* var. *ovata* (E.Mey.) B.J.Pienaar and *V. vexillata* var. *davyi*

(Bolus) B.J. Pienaar (Pienaar & Kok 1991). The main diagnostic differences (summarised in Table 1) among these varieties involve the indumentum of the leaves: primarily aculeate in *V. vexillata* var. *angustifolia*, thick setaceous bristles in *V. vexillata* var. *davyi*, velutinous in *V. vexillata* var. *ovata* and tomentose-hirsute or hispid in *V. vexillata* var. *vexillata*. Furthermore, *V. vexillata* var. *davyi* has uni-, bi- and tripinnate leaves while the other varieties all have strictly tripinnate leaves (Verdcourt 1970; Maréchal et al. 1978a; Pienaar & Kok 1991). Although some leaf characters overlap among the varieties, the leaf base of the terminal leaflet is distinct in *V. vexillata* var. *vexillata* (cuneate to rounded or obtuse) and *angustifolia* (truncate) (Wilczek 1954). *Vigna vexillata* prefers to grow on southern slopes (Pienaar & Kok 1991) at altitudes ranging from 0 to 2 500 m (particularly *V. vexillata* var. *angustifolia* and *vexillata*). While *V. vexillata* var. *vexillata* is widely distributed across grasslands, thickets, bushlands and forests (Verdcourt 1971), *V. vexillata* var. *angustifolia* thrives mainly in grasslands (Verdcourt 1971), var. *ovata* in grasslands and var. *davyi* in rocky grass hillslopes on southwestern aspects. Moreover, *V. vexillata* generally prefers to grow in disturbed habitats such as channels along the roads, dams and tracks that are usually walked over by cattle (Pienaar & Kok 1991).

According to Pienaar & Kok (1991), *Vigna vexillata* is a food and forage crop. The young leaves, pods and rootstocks are consumed in many African cultures, while the root is often fed to goats to increase milk production. The tubers contain about 15% protein, making it a more nutritious root crop than e.g., cassava (3%), potato (5%), sweet potato (5%) and yam (6%) (Vanderborght 1989). *Vigna vexillata* has been reported to contain beneficial genetic makeup that allows it to thrive in unfavourable agricultural areas (Takahashi et al. 2016), resist floods and pest attacks, in particular the seeds, due to the presence of an essential dipeptide, para-aminophenylalaline, which serves as a defence mechanism against parasitic beetles (Vanderborght 1989; Miller & Williams 1981; Birch et al. 1986; Ogundiwin et al. 2002).

Table 1. Diagnostic differences among the four varieties of *Vigna vexillata* in southern Africa

| Characters                           | var. <i>angustifolia</i>        | var. <i>davyi</i>                     | var. <i>ovata</i>                                            | var. <i>vexillata</i>                                        |
|--------------------------------------|---------------------------------|---------------------------------------|--------------------------------------------------------------|--------------------------------------------------------------|
| <b>Leaflet shape</b>                 | Linear-lanceolate               | More or less rhombic to broadly ovate | Obtuse to narrowly or broadly ovate                          | Ovate to elliptic or slightly lanceolate                     |
| <b>Leaflet base shape</b>            | Truncate to obtuse              | Broadly obtuse to cuneate             | Obtuse                                                       | Cuneate to more or less obtuse                               |
| <b>Leaflet apex shape</b>            | Acuminate                       | Acuminate                             | Obtuse and often apiculate                                   | Usually acute                                                |
| <b>Leaflet arrangement</b>           | Tripinnate                      | Uni-, bi-, or tripinnate              | Tripinnate                                                   | Tripinnate                                                   |
| <b>Leaflet indumentum</b>            | Aculeate                        | Setaceous                             | Velutinous                                                   | Tomentose-hirsute or hispid                                  |
| <b>Calyx lobe versus tube length</b> | Lobes usually shorter than tube | Lobes up to twice as long as tube     | Lobes usually longer than tube but not twice as long as tube | Lobes usually longer than tube but not twice as long as tube |

*Vigna vexillata* has a specialised pollination mechanism referred to as ‘hugging pollination’, which was first described by Hedström & Thulin (1986) and later by Pienaar & Kok (1991). The keel of *V. vexillata* is twisted through 180° towards the left, causing the internal reproductive organs (androecium and gynoecium) to also twist. The pollinator (bee) lands on the left-hand wing petal and gains a foothold using the lamellar structures at the bottom of the wing blades. It then pushes its head downwards between the two calli towards the base of the standard petal to slide its proboscis through the narrow area linking the standard claw and the bottom of the superior stamen to reach the nectary at the base of the ovary (Hedström & Thulin 1986; Pienaar & Kok 1991; Delgado-Salinas et al. 2011). The weight of the bee, and the pressure it applies to reach the nectary, causes the left-hand wing petal to push against the interlocked left-hand keel petal, forcing it to curve around the insect while the style and stamens protrude from the inflexible keel beak. The keel then ‘hugs’ the body of the pollinator on the upper lateral part of the head and thorax (Hedström & Thulin 1986; Pienaar & Kok 1991). If the body of the bee has pollen from a previously visited flower, it will deposit the pollen onto the stigma. Concurrently, pollen from the presently visited flower will be rubbed onto the body of the bee to enable cross pollination (Pienaar & Kok 1991). This mechanism may be a key factor in preventing *V. vexillata* from cross-pollinating with other species with a flat keel. The main flowering and fruiting time for *V. vexillata* is between October and April, although flowering and fruiting may occur throughout the year.

**Description** (for *Vigna vexillata*; see discussion and Table 1 for differences among the four southern African varieties).—Plants perennial with herbaceous stems, climbing or creeping, variously ferruginous, aculeate, hispid, setaceous, tomentose-hirsute or velutinous; roots fusiform. *Stipules* ovate to lanceolate, medifixed, base cordate-bi-auriculate, apex acuminate, 2–13 × (0.5–)1.0–4.0 mm, densely tomentose to strigose, or pubescent, glabrescent; stipels lanceolate, base more or less rounded, apex acuminate, 0.2–4.0 × 0.1–1.0(–3.0) mm, indumentum similar to stipules. *Leaves* mono-, bi-, or tripinnate; rachis 0.4–8.0(–17.0) × ± 0.5(–1.0) mm or sessile in unipinnate leaves; petiole (1.5–)6.0–110.0 mm long, indumentum similar to stems; petiolule 1–2(–3) mm × 0.5–0.9(–1.0) mm, indumentum similar to stems but generally more dense; leaflets linear-lanceolate, elliptic, narrowly to broadly ovate or rhombic, leaflet bases cuneate, obtuse or truncate, leaflet apices acute, acuminate or obtuse and apiculate, terminal leaflet 10–135(–150) × 4–56(–67) mm, lateral leaflets 13–115(–120) × 4–44 mm, hairy on both leaflet surfaces, glabrescent. *Inflorescences* axillary with 2–3(–4) flowers (subtended by 2–4 extrafloral nectaries), 15–23 × 8–21 mm; petals whitish-cream, to mauve, pink, purple or pale yellow-green; peduncles 50–153(–179) × 1–2(–4) mm, indumentum same as stems; pedicels 1–2 mm long; bracts 3–9 × 0.5–3.0 mm, caducous; bracteoles 2–6 × ± 0.5–1.0 mm, caducous; calyx subequally lobed, ± 5–15 mm long, tube ± 4–± 12 mm long, upper lobes 3–6(–8) × 1–3 mm, lower lobes ± 4.5–6.5(–10.0) × 1–3 mm, lobes shorter than or up to twice as long as the tube, indumentum ferruginous or pubescent and glabrescent; standard lamina rotund and obovate, apex emarginate, 11–29 × 12–35 mm, glabrous; wings more or less obovate to oblong and auriculate, apex obtuse, 7–24 × 5–18 mm, glabrous, smooth or sometimes with sculpturing; keel rostrate, keel beak twisted towards the left through 180°, 7–23 × 5–15 mm, glabrous, with a pocket present on the left-hand petal, 3–5 × 2.5–3.5 mm. *Androecium* diadelphous, 9 filaments fused and 1 free, all curved to the right. *Gynoecium* sessile, linear-cylindrical; ovary densely hirsute to pubescent, surrounded by a short nectariferous disc; style linear and curved towards the left (like the keel) with dense hairs distributed along the upper side,

appearing upside down when protruding from the flower; stigma capitate. *Fruits* linear-cylindrical, 40–119(–140) × 2–5 mm, heavily ferruginous, densely pubescent to puberulent in all varieties, ± 9–25-seeded. Seeds reniform to spherical or cubic, 2–6 × 2–3 mm, dark red to maroon to darkish-brown, mottled black to maroon; rim aril present, light to dark brown to black; hilum elongate; epihilum present, cream to yellow. Plate 2393.

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*Lasiosiphon polycephalus*

## Thymelaeaceae

*Botswana, Namibia, South Africa*

***Lasiosiphon polycephalus*** (E.Mey. ex Meisn.) H.Pearson in Flora of Tropical Africa 6(1.2): 228 (1913). *Passerina polycephala* E.Mey. ex Meisn.: 390 (1841). *Arthrosolen polycephalus* (E.Mey. ex Meisn.) C.A.Mey.: 359 (1843); Wright: 4 (1915). *Gnidia polycephala* (E.Mey. ex Meisn.) Gilg ex Engl.: 138 (1894).

Thymelaeaceae are a medium-sized family of small trees and mostly shrubs that was first established by French botanist Antoine Laurent de Jussieu (De Jussieu 1789). He is notable for being the first botanist to publish a natural classification of flowering plants, with numerous present day plant families still attributed to his initial work. The family name Thymelaeaceae was derived from the genus name *Thymelaea* Mill., a combination of the Greek words *thúmos* (θύμος), which means ‘thyme’, and *elaía* (ἐλαία) meaning ‘olive’ (Chittenden 1965). The name alludes to characteristics of members of the family, in that they have foliage that is reminiscent of thyme, while the fruits are similar in appearance to olives (Chittenden 1965). Thymelaeaceae are cosmopolitan and most common in temperate and tropical regions of the globe (Koekemoer et al. 2014). The family is well represented in southern Africa, with nine genera comprising  $\pm$  190 species (Beaumont et al. 2009; Bredenkamp & Beyers 2000). The family is especially diverse in the winter-rainfall regions of the Western Cape, South Africa (Koekemoer et al. 2014).

The main diagnostic characters of the family Thymelaeaceae are their tough, fibrous bark, with leaves that are either opposite or alternate, sometimes needle-like, and lacking stipules. The flowers are tubular and mostly regular, sometimes in dense, involucrate heads. The petals or petaloid scales are either inconspicuous or absent, and the fruits are either achenes, berries or drupes (Koekemoer et al. 2014).

The phylogenetic analysis of nuclear and plastid DNA sequences for a selection of species of *Gnidia* L. and allied genera by Van der Bank et al. (2002) showed that substantial revision of the generic circumscriptions for the subfamily Thymelaeoideae was necessary to render the genera monophyletic – especially for the diverse genus *Gnidia*, which included more than 140 species in tropical and southern Africa and Madagascar (Beaumont et al. 2009). *Gnidia*, as previously circumscribed, was shown to be highly polyphyletic and included at least four distinct lineages scattered throughout the Thymelaeoideae (Manning & Boatwright 2013). As a first step towards a monophyletic generic classification of the subfamily, Beaumont et al. (2009) reinstated the genus *Lasiosiphon* Fresen., as this clade was strongly supported and well separated from the remaining *Gnidia* species by a clade comprising the genera *Dirca* L., *Ovidia* Raf., *Peddiea* Harv. and *Stephanodaphne* Baill. Subsequent authors have followed this treatment by providing additional combinations for the southern African species, some of which were not yet named within *Lasiosiphon* (Manning & Boatwright 2013; Magee & Manning 2017).



PLATE 2394 *Laiosiphon polycephalus*



*Lasiosiphon* was originally morphologically distinguished from *Gnidia* and allied tetramerous genera by its pentamerous flowers (Fresenius 1838). The genus was subsequently included in *Gnidia* by Peterson (1959, 1978) on account of the evident instability of this character (Boatwright et al. 2017). Secondary characters diagnostic of *Lasiosiphon* are the capitate, involucrate inflorescences subtended by foliaceous or petaloid bracts, the pubescent hypanthium, and the waxy, bright yellow to orange or red hypanthium lobes (Magee & Manning 2017). With the inclusion of tetramerous species, the genus is diagnosable only by a combination of characters. Like *Gnidia*, it also includes some species with ebracteate, few-flowered inflorescences plus taxa with and without petaloid scales in the mouth of the hypanthium (Beaumont et al. 2009). *Lasiosiphon* currently numbers some 35 species from Africa and Madagascar, with  $\pm 20$  recorded in southern Africa (Magee & Manning 2017).

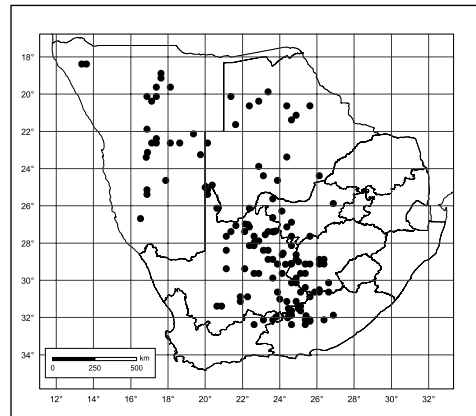


FIGURE 1.—Known geographical distribution range of *Lasiosiphon polycephalus* in southern Africa.

The southern African species fall into two morphological groups: (1) pentamerous species with a foliaceous involucre and a hypanthium tube lacking long stiff hairs at the base; and (2) pentamerous or tetramerous species with a pedunculate capitulum and a papery, coloured involucre, and a hypanthium tube that is strongly bearded at the base with long, stiff hairs. Most of the southern African species, with the notable exception of *Lasiosiphon pedunculatus* (Beyers) J.C.Manning & Boatwr., are pentamerous. A few of the Madagascan species have ebracteate, few-flowered inflorescences (Rogers 2009). The genus *Arthrosolen* C.A.Mey. (1843), originally described for those *Gnidia*-like species lacking petaloid scales, included a disparate group of unrelated taxa. It was subsequently redefined by Phillips (1944, 1951) to include only those species with pedunculate, capitate inflorescences surrounded by an involucre of enlarged, membranous and often coloured bracts, and in this circumscription it is inseparable from *Lasiosiphon*. Among the southern African species of *Lasiosiphon*, just a handful are characterised by their twiggy habit and small, glabrous leaves, notably *L. microphyllus* (Meisn.) Meisn., *L. rigidus* J.C.Manning & Boatwr., *L. suavis-simus* (Dinter) Domke, *L. esterhuyseniae* Magee & J.C.Manning and *L. polycephalus*.

*Lasiosiphon polycephalus* (Figures 1 & 2) has a distribution ranging from Botswana and Namibia to South Africa (Figure 1). In South Africa, *L. polycephalus* is distributed mainly throughout the Northern Cape, North West, Free State, Eastern Cape and Western Cape provinces. Populations of *L. polycephalus* have been recorded in a variety of habitats in South Africa, at altitudes from 600–1 160 m, including various types of shrubland and grassland, broken veld, Karoo hardeveld, mountain bushveld, duneveld, thornveld, vaalbosveld and alluvial vegetation (Koekemoer et al. 2014; Von Staden 2015). *Lasiosiphon polycephalus* has several vernacular names in English: January bush, summer curryflower; and in Afrikaans: besembossie, janewariebos, jannewariebos, januariebos, perdebossie and waaibossie



FIGURE 2.—*Laiosiphon polycephalus* on a farm in the Pixley ka Seme District, Northern Cape Province, South Africa: a, entire plant in habitat; b, multiple flowering stems; c, flowering branch. Photographs: a–c, N. van Berkel.

(Von Staden 2015). In Setswana, *L. polycephalus* is called *makgonasotlhe* (Munkombwe et al. 2003).

Beaumont et al. (2001) speculate that the papery involucre bracts in the species aid in protecting developing flowers, possibly by regulating temperature. The bracts are also frequently imbricate and encapsulate the ovaries and hypanthial tubes affording protection to nectar resources and developing ovaries (Beaumont 2010). Pollination studies in the Thymelaeoideae are limited, but the genera *Thymelaea* (El-Keblawy et al. 1996; El-Keblawy & Freeman 1999; Cornara et al. 2005) and *Struthiola* L. (Makholela & Manning 2006) have been investigated to some extent. Thymelaeoideae are primarily entomophilous, with wind- and bird-pollination uncommon (Beaumont 2010). The tubular flowers of most *Gnidia* and *Struthiola* species are also sweetly scented at night and have been reported to attract moths as pollinators (Koekemoer et al. 2014). Butterfly pollination has been recorded for *Lasiosiphon kraussianus* (Meisn.) Meisn. and beetle pollination for *L. eriocephalus* Decne. (Henning 1984; Somanathan et al. 2004). However, more pollinator studies need to be conducted for *Lasiosiphon* species to shed light on the major pollinators associated with the genus and also if any pollination syndromes may exist.

The roots of *Gnidia* species and allied genera are reportedly used to treat several ailments such as constipation, boils, burns, snakebites, coughs, insanity and poor appetite (Mothogoane 2013). *Lasiosiphon polycephalus*, in particular, is commonly used in traditional medicine and is prepared in numerous ways that can be ingested orally for supposedly stabilising heart conditions, treatment of tuberculosis and tonsillitis, and the ashes can also be applied onto wounds (Hedberg & Staugard 1989). However, the plant has also been reported to be toxic and even lethal when ingested by livestock, which often feed on it because of its prevalence and freshness in arid areas (Kellerman et al. 1988). Daphnetoxin, a daphnane-type orthoester diterpene found in plants belonging to the family Thymelaeaceae, is present in *L. polycephalus*. When ingested, the compound can cause diarrhoea in ruminants and humans, accompanied by emphysema, which causes polypnoea (Botha & Penrith 2008). Other risks and complications of ingesting daphnetoxin include deleterious effects on the kidneys, central nervous system and circulatory system (Mbaveng et al. 2014). Other phytochemicals that have been isolated from *L. polycephalus* include umbelliferone and two glycosides (Rindl 1917, 1933; Vermeulen & Pieterse 1968), one of which was characterised as yuankanin (Ragot et al. 1988). Munkombwe et al. (2003) also reported isolating phenylpropanoid glycosides along with syringin and adicardin from stems of *L. polycephalus*.

Some of the yellow-flowered *Gnidia* species have historically been used to dye leather and wool. The Khoisan also used the stringy bark to tie bundles of wood together (Koekemoer et al. 2014).

*Gnidia* and *Lasiosiphon* species are not well-known among the general public and not often cultivated, apart from *G. squarrosa* (L.) Druce, which is often used in fynbos and coastal gardens (Notten 2004), and *Gnidia virescens* Wikstr. which is cultivated in specialist greenhouses in Europe (Peterson 2006). The most widely cultivated southern African member of the Thymelaeaceae is *Dais cotinifolia* L. (pompontree) (Bredenkamp 2002). This ornamental tree is well known in gardens (Phillips 1942; Palmer & Pitman 1961; Koekemoer

et al. 2014). Other Thymelaeaceae that have been successfully cultivated include *Passerina filiformis* L. in Britain and Europe since the eighteenth century and *Passerina obtusifolia* Thoday in the Western Cape Province for the wild-flower industry (Bredenkamp 2002). Techniques used in the cultivation of other species from the family Thymelaeaceae may be useful in promoting cultivation of *Lasiosiphon* species in horticulture. For instance, *Pimelea* Banks ex Gaertn. species have been reported to respond well to pruning (Elliot & Jones 1997) and tip pruning of *P. ciliata* Rye has been found to encourage compact growth and even flowering, thereby making this species suitable as a pot plant (Slater et al. 1994). Many of the South African species of *Lasiosiphon*, especially those that share a similar habit such as *L. microphyllus*, *L. rigidus*, *L. suavissimus*, *L. esterhuyseniae* and *L. polycephalus*, develop long, bare and unattractive stems with leaves and flowers clustered at the ends of branches (Magee & Manning 2017). Tip pruning of these species may promote bushiness and increase their attractiveness as garden subjects (Beaumont 2010).

**Description.**—A small, virgate subshrub,  $\pm 0.6$  m high, with erect, glaucous branches. Leaves scattered, erect, linear, 1-nerved and narrowed at both ends, subacute,  $6.0\text{--}13.7 \times 1\text{--}2$  mm. Heads ovoid, few-flowered, pedunculate, terminal; involucre bracts  $\pm 9$ , erect, ovate or triangular-ovate, rounded at the base, acute, obtuse or rounded at apex, silky-pubescent adaxially, the inner bracts  $\pm 13 \times 9$  mm, outer smaller. Flowers 5-merous, yellow, pedicelled; pedicel  $\pm 1.6$  mm long, with ring of erect, silky hairs at summit. *Hypanthium* tube slender, pubescent above articulation, densely villous with long, erect, silky hairs below,  $\pm 13$  mm long; lobes spreading, oblong, obtuse or subacute, densely pubescent on lower surface,  $\pm 3$  mm long. *Anthers* oblong, 1.6 mm long. *Ovary* glabrous; style  $\pm 3$  mm long; stigma cylindrical. *Fruit* ovoid,  $\pm 4$  mm long; pericarp thin, black, brittle; testa thin; embryo large, 3–4 mm long. *Flowering time*: July through to October. Plate 2394.

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PLATE 2395 *Strychnos pungens*

*Strychnos pungens*

Loganiaceae

*Tropical and subtropical Africa*

***Strychnos pungens*** Soler. in Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 17: 554 (1893). *Strychnos occidentalis* Soler.: 40 (1892). *Strychnos henriquesiana* Baker: 86 (1893). *Strychnos sapinii* De Wild.: 382 (1910). *Strychnos brazzavillensis* A.Chev.: 136 (1911).

The genus *Strychnos* L. consists of 204 accepted species that are widely distributed around the tropics and subtropics (Kew Plants of the World Online 2022). The genus name was derived from the Greek word meaning ‘deadly’, which refers to the toxic properties that are found in some of the species, but more specifically the toxin strychnine, which is found in the seeds of *Strychnos nux-vomica* L., a species described by Linnaeus in his *Species Plantarum* in 1753. Members of this genus are found throughout Africa, as well as in Australia, Asia, the East-Indies and South America (Coates Palgrave 2002; Schmidt et al. 2002).

*Strychnos pungens* was placed in the family Loganiaceae when it was first described (Solereder 1893). Loganiaceae were initially recognised as one of six families in the order Gentianales (Lindley 1833; Bentham 1856; Bentham & Hooker 1876). Takhtajan (1987, 1997) later described nine families within the order Gentianales and in this system, Loganiaceae were separated into Loganiaceae and Strychnaceae based on apparent polyphyly recorded in work by Leeuwenberg & Leenhouts (1980). As a result, some botanists recognise *Strychnos* within the family Strychnaceae. The Strychnaceae were first described by Perleb in 1818 but Backlund et al. (2002) concluded that Strychnaceae could not be retained (in accordance with Struwe et al. 1994), due to similarities in the iridoid compound formation processes common to members of Loganiaceae. Furthermore, DNA-based studies indicate *Strychnos* is sister to *Spigelia*, which is considered to be a member of the Loganiaceae (Backlund et al. 2000; Takhtajan 1987, 1997), therefore suggesting that *Strychnos* should also be classified within the Loganiaceae.

*Strychnos pungens* and *S. occidentalis* were first briefly described by Hans Solereder in 1893 (Backlund et al. 2000), but *S. occidentalis* was later reduced to a synonym of *S. pungens* in the formal description in 1893 (Leeuwenberg 1969). *Strychnos henriquesiana* (Baker 1893), *S. sapinii* (De Wildeman 1910) and *S. brazzavillensis* (Chevalier 1911) were initially described as new species but were later reduced to synonyms of *S. pungens*.

*Strychnos pungens* is a deciduous tree with a shrub-like appearance (Leeuwenberg 1983), found in the semi-arid regions of southern and southern tropical Africa (Ntcheu Ngemakwe et al. 2017). It is generally 1 to 7 metres tall and produce hard, orange-like fruits. It is easily distinguished from other species in the genus by the presence of small spines at the end of the leaves, hence the specific epithet *pungens* (Dyer et al. 1963) (Figure 1).

PLATE 2395.—1, flowering branch, × 1; 2, fruiting branch, × 1. Voucher specimens: M. Momberg & A. Frisby 188 and M. Momberg & A. Frisby 189 in H.G.W.J. Schweickhardt Herbarium (PRU), Pretoria. Artist: Lesley Deysel.



FIGURE 1.—*Strychnos pungens* in habitat: a, whole tree at Mahamba, Eswatini; b, leafy shoot showing characteristic leaf venation of a tree in Faerie Glen Nature Reserve, Pretoria; c, cluster of flowers on tree growing near Bela Bela; d, unripe fruit and branches of a tree on Mamelodi Ridge, Pretoria. Photographs: a, L. Löffler; b, M. Roberts; c, A.E. van Wyk; d, N.P. Barker.

Flowers are produced during October and fruits ripen between March and August, at which point they are suitable for human consumption (Coates Palgrave 2002; Schmidt et al. 2002). The species is relatively drought resistant, but it may become dormant during periods of extreme drought (Nitcheu Ngemakwe et al. 2017). Its Red List status is Least Concern (Foden & Potter 2005).

A species-level DNA-based study resolved *Strychnos pungens* as belonging to section *Densiflorae*, along with *S. madagascariensis* Poir. and *S. gerrardii* N.E.Br. These species (as well as some others in section *Spinosa*) all produce large, hard fruits (Adebowale et al. 2016).

*Strychnos pungens* is indigenous to tropical and subtropical Africa. It occurs in the southern African countries of Botswana, Namibia, Zambia and Zimbabwe (Leeuwenberg 1983; Schmidt et al. 2002) and within South Africa it is found in the provinces of Mpumalanga, Gauteng, Limpopo and North West (Figure 2) where it occurs in the Savanna Biome. An observation on iNaturalist (2019) suggests that the distribution range extends into the south-western area of Eswatini (Figure 1a). It occupies habitats that are often classified as semi-arid areas, with soils being generally coarse and sandy. Trees are commonly found in rocky areas and at the bases of rocky hills. In northeastern Namibian woodlands it dominates the shrub layer (Sheuyange et al. 2005). It has also been observed on Kalahari sand dunes (Dyer et al. 1963; Coates Palgrave et al. 2002; Schmidt et al. 2002). Average annual rainfall for these areas range between 500 and 600 mm in the summer months (Sheuyange et al. 2005).

Because of the relatively wide distribution of the species, it has a number of vernacular names from the various languages spoken throughout its range. These include spine-leaved monkey-orange (English); *stekelblaarklapper* (Afrikaans), *mukubuda* (Venda), *mudo*, *mugwati*, *mumbumi*, *mutamba-usiku* (Shona), and *umgwadi*, *umgwai* (Northern Ndebele). Once a common plant in the Pretoria area, Klapperkop received its name from the abundance of *klapper* trees growing on and around it (Dyer et al. 1963).

The plant has been utilised by generations of traditional healers, tribes and local communities across its geographical range, mostly for its medicinal properties, although various other uses have been recorded. The Mbukushu tribe in Kavango, Namibia treat dysentery by boiling fresh root bark in water and consuming it as a tea, while communities in north-western Namibia crush the root and use it as a treatment for bone diseases (Mannheimer & Curtis 2009). Some tribes in Namibia use the unripe fruit as poison for arrow tips when mixed and boiled with snake venom and other plant- and insect-based ingredients (Bradfield et al. 2015). The fruits are further used to treat sexually transmitted diseases and has also been used in the Zulu culture as an antidote for snakebites (Nitcheu Ngemakwe et al. 2017). Boiled root bark is used to treat stomach ache and bronchitis, and lotions from crushed leaves and water is used to treat eye sores (Coates Palgrave et al. 2002). In natural environments, such as reserves and city parks, this species is an important year-round food source for various browsers, especially in the dry season because it is one of the few species that retain its leaves (Owen-Smith & Cooper 1987).

The wood is whitish, hard and straight, making it a preferred species among the Zulu people, who use the wood for walking and fighting sticks (National Research Council 2008).

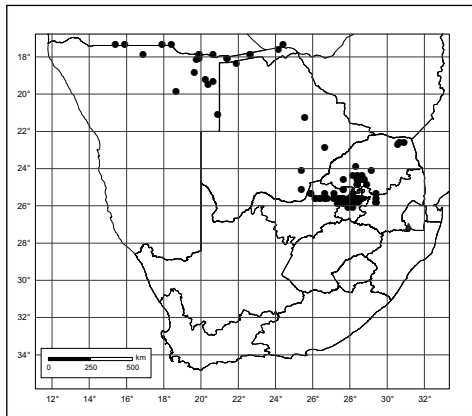


FIGURE 2.—Distribution of *Strychnos pungens* in southern Africa. The locality in Eswatini (triangle) indicates an image identified from iNaturalist ([www.inaturalist.org/observations/20303300](http://www.inaturalist.org/observations/20303300)) with no voucher specimen.

The hard, dried outer shells of the fruit are sometimes used as cups, containers for small items or baby rattles (Curtis & Mannheimer 2005).

Pharmacological analyses have shown that the pulp of *Strychnos pungens* has moderate to good antimicrobial activity against numerous bacteria and fungi, including those responsible for causing typhoid fever (*Salmonella typhi*), scarlet fever (*Streptococcus pyogenes*), food poisoning (*Bacillus cereus*) and pneumonia (*Klebsiella pneumoniae*) (Tshikalange et al. 2017). Various species of *Strychnos* have been tested for potential use in malaria treatment and, although some showed promising results, *S. pungens* appeared to have no effect (Philippe et al. 2005).

*Strychnos* species also have great potential to become a sustainable source of food in rural African communities because of their high fruit yield, nutritious properties and high tolerance to drought. According to the National Research Council (2008), at least 20 species of *Strychnos* produce edible fruit with the three most widely used species being *S. cocculoides* Baker, *S. spinosa* Lam. and *S. pungens*. The fruit from *S. pungens* contain carbohydrates, protein, fibre and various other minerals, vitamins and nutrients (Ngadze et al. 2017). It has been suggested that the cultivation of this species could serve as a food source for many local communities when harvests from cultivated crops are poor, and therefore act as a buffer against hunger and malnutrition (Mukwada 2008; Ngadze et al. 2017; Nitchau Ngemakwe et al. 2017). However, consumption of unripe fruit has been known to cause headaches, nausea and vomiting (Schmidt et al. 2002). Furthermore, Curtis & Mannheimer (2005) comment that the fruits of *S. pungens* are not as tasty as those of *S. cocculoides*.

**Description.**—Small deciduous tree with shrub-like appearance, 2–7 m high. *Trunk* 0.1–0.2 m in diameter or larger; bark usually grey or brown with rough texture, close reticulation present, not corky; wood and inner bark yellowish. *Branches* pale to dark brown with abundance of lenticels, lacks parallel grooves, usually hairless and smooth; younger bark greyer. *Branchlets* thick, swollen at nodes with rough, corky texture, usually 2–4 mm in diameter with slightly prominent sub-erect leaf bases. *Leaves* 30–80 × 10–35 mm, rigid, elliptic, leathery; lamina dark green and shiny, duller abaxially, usually glabrous; apex sharply pointed and spine-tipped; base rounded or wedge-shaped; petioles 1–4 mm long, glabrous; primary veins prominent, in 3s from leaf base, 1 pair of secondary veins and network of tertiary veins usually present. *Inflorescences* axillary cymes on older branches. *Flowers* packed closely together with short stiff pedicels, single terminal flower, pentamerous. *Calyx* 7.0–9.5 mm long; sepals green, loosely attached, ovate, 2–4 × 2–3 mm, with conspicuous cilia. *Corolla* tube cylindrical, 3 mm long, inner section covered with ring of white, woolly hairs, glabrous toward tips; petals greenish cream to yellow, thick, narrowly

triangular with acute spreading apices, 3 mm long. *Stamens* filamentous, glabrous, attached at mouth of corolla tube, slightly protruding; anthers oblong, glabrous, 1–2 mm long. *Pistil* 5.0–7.5 mm long; ovary two-celled,  $\pm$  25–60 ovules per cell, oblong,  $1-3 \times 0.7-2.0$  mm, usually disc-shaped base, long soft hairs present at apex; style thick, 2.5–4.5 mm long with hairy base; stigma with distinct head. *Fruit* blue-green maturing to orange or yellow, 50–150 mm in diameter, globose with slightly granular texture and shine, weight  $\pm$  145–383 g; outer shell thick, hard, woody when dried; pulp sweet-tasting, yellow, contains 20–100 seeds. Seeds ochre, flattened and elliptic or obliquely ovate, rough with short, hard hairs present,  $20-24 \times 5-10$  mm. Plate 2395.

### ACKNOWLEDGEMENTS

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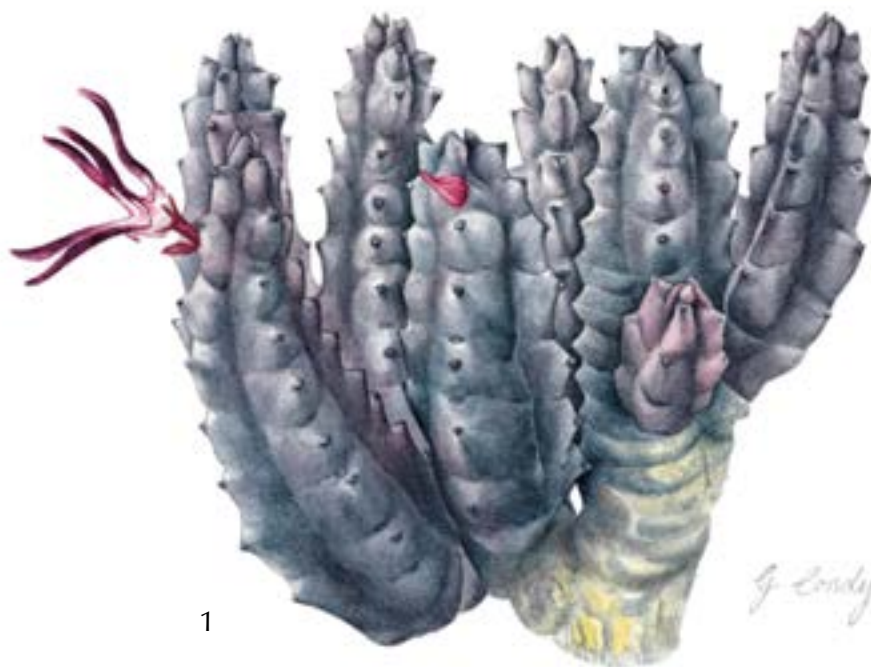
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G. Condy

*Ceropegia lineariloba* Apocynaceae: Asclepiadoideae: Ceropegieae

South Africa

***Ceropegia lineariloba*** Bruyns in South African Journal of Botany 112: 399 (2017). *Quaqua linearis* (N.E.Br.) Bruyns: 33 (1983). *Caralluma linearis* N.E.Br. t. 1905a (1891).

*Ceropegia* L., of the family Apocynaceae, subfamily Asclepiadoideae is the largest genus of the tribe Ceropegieae and has recently been the subject of much taxonomic research. Meve & Liede (2004) divided the tribe Ceropegieae into four subtribes. Of these, the Stapeliinae includes the stapeliads, as well as *Brachystelma* R.Br. and *Ceropegia*.

*Ceropogia* was described by Linnaeus (1753) in his landmark publication *Species Plantarum*. According to Linnaeus, *Ceropegia* was mainly characterised by its tubular flowers and, among the species that he recognised, he included two that were subsequently transferred to *Microlooma* R.Br. *Ceropegia* was revised by Huber (1957), who reduced the number of species to 153 and placed them in 21 sections. However, this taxonomic arrangement of sections has not been widely used in southern Africa, since Dyer (1980) believed that Huber's overemphasis on pubescence of the vegetative and floral parts had led to an 'unnatural' arrangement.

Since then, the taxonomy of *Ceropegia* has been nothing if not controversial. As with many large genera, the generic limits of *Ceropegia* have been questioned as a consequence of various DNA-based molecular phylogenetic studies. In this context, it is particularly important to note that all phylogenetic treatments that have included representatives of all three of the 'groups' *Ceropegia*, *Brachystelma* and the stapeliads, have shown that both *Brachystelma* and the stapeliads are nested within *Ceropegia* (Figure 1). This was first shown over 20 years ago in the preliminary investigations of Meve & Liede (2002) using only two gene regions. Similar results were obtained in the relatively limited sampling of Meve & Liede (2004) and once again by Meve & Liede-Schumann (2007). In an era where monophyly generally dictates taxonomic and nomenclatural changes (Potter & Freudenstein 2005), these authors concluded that, although both *Brachystelma* and the stapeliads were nested within *Ceropegia*, *Ceropegia* nevertheless remained 'taxonomically sound', but in this context it is paraphyletic. This overlooks many parallel developments in vegetative and floral features in all three groups, which make the three groups difficult to separate and cause problems in precisely defining many of the stapeliad genera. This is explained in detail in Bruyns et al. (2017), who adhered to the application of monophyly in delimiting genera.

Surveswaran et al. (2009) added new data from the Indian subcontinent and provided a better-sampled phylogeny, which showed, contrary to all previous assumptions, that

PLATE 2396.—1, plant (roots not shown), × 1; 2, frontal view of flower, × 3; 3, frontal view of gynostegium, × 10; 4, side view of gynostegium, × 10; 5, pollinarium, × 25. Voucher specimen: Pretoria National Botanical Garden 26453 (living collection), collected by T.J. Coetzee, Touws River, October 1981. Artist: Gillian Condy.

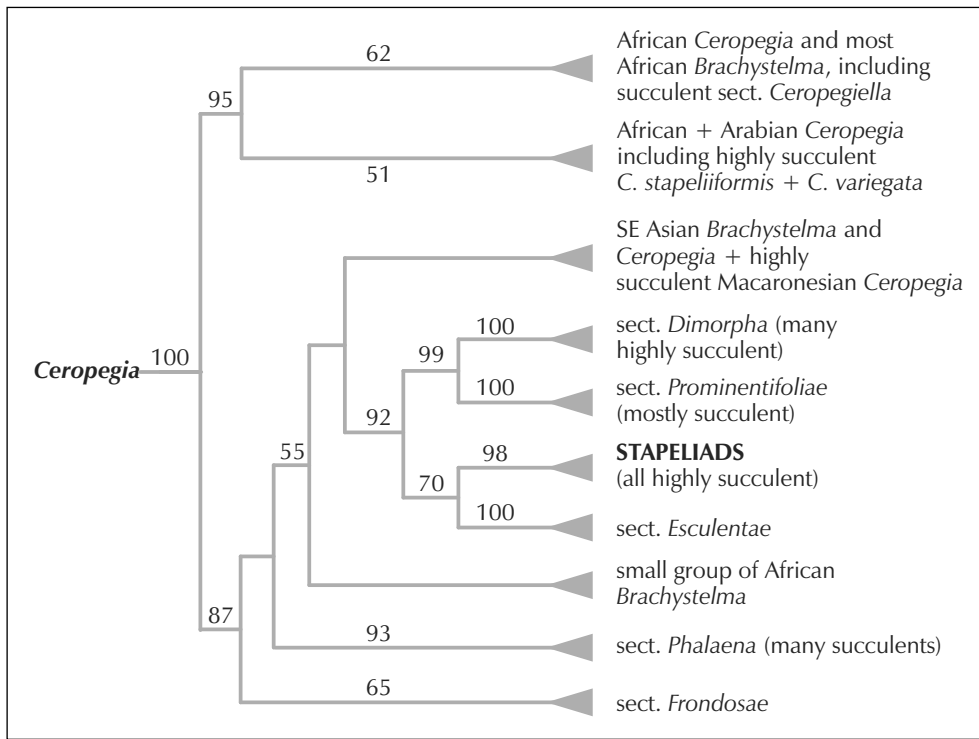


FIGURE 1.—Simplified cladogram from Bruyns et al. (2015), showing the whole of *Ceropegia* in the new and expanded sense and showing the manner in which the stapeliads are nested within *Ceropegia*. This was obtained using DNA-data and maximum likelihood analysis (numbers above branches indicate bootstrap percentages where > 50%). Some of the sections of *Ceropegia* among which the stapeliads are embedded are indicated. It also shows the extent to which succulents are distributed among the many clades in *Ceropegia*. Note that the area of the triangles does not reflect the number of species in each group.

*Brachystelma* does not consist of a single lineage within *Ceropegia*, but at least two lineages, namely an Indian and an African lineage. Alongside this, they also found that the stapeliads were again nested within *Ceropegia*. With improved sampling of *Brachystelma* and *Ceropegia*, Bruyns et al. (2015) showed that *Brachystelma* consisted of at least four lineages and, as previously found, the stapeliads were nested in *Ceropegia* and their closest relatives in *Ceropegia* were identified. The same was shown once more by Surveswaran et al. (2021) who found additional lineages of Southeast Asian *Brachystelma*.

The conclusion from the various analyses justifies the sinking of both *Brachystelma* and the stapeliads into *Ceropegia* as done by Bruyns et al. (2017). An alternative taxonomic approach would be to recognise this one, large, monophyletic genus and divide *Ceropegia* and *Brachystelma* into smaller monophyletic units. However, this would necessitate the creation of many new genera that would be extremely difficult to recognise and delimit on the basis of morphology. In addition, this solution would cause great nomenclatural instability, since *Ceropegia* itself would have to be broken into many smaller units. Endress et al. (2018) and Goyder et al. (2020) suggested a third approach, which Styles & Meve (2021) explained

as follows: ‘based on phylogenetic analyses and substantial morphological similarities with regard to root-systems, stems and leaves, Endress et al. (2018) regarded only the inclusion of *Brachystelma* in[to] *Ceropegia* [as] justifiable, whereas the monophyletic and morphologically well-defined stem-succulent stapeliads are kept separate with all their genera’. However, no new evidence was presented to substantiate this statement or to justify the rejection of the new monophyletic concept for *Ceropegia* of Bruyns et al. (2017).

Therefore, all relevant phylogenetic analyses conducted to date show that if *Brachystelma* is included in *Ceropegia* then, based on the concept of monophyly, the stapeliads should be included as well. Morphological data also support this approach. Furthermore, this classification expresses clearly how the remarkable diversity in succulence in the stapeliads has evolved among the many non-succulent lineages of *Ceropegia*. Treating *Ceropegia* in isolation does not clarify the origin of this trait. The classification of Bruyns et al. (2017) therefore not only reflects the evolutionary history of the group, but also allows for a more stable classification in the long term by having adopted a broader generic concept. Adopting a monophyletic approach and recognising an expanded *Ceropegia* aligns with other recent treatments in the Apocynaceae, which have strived to recognise monophyletic rather than paraphyletic entities. Examples include the new family concept where the Asclepiadaceae was included in the Apocynaceae to achieve monophyly (Endress & Bruyns 2000), the considerable expansion of *Cynanchum* L. to re-establish monophyly (Khanum et al. 2016), the recent re-establishment of monophyly by moving the  $\pm$  300 species of *Tylophora* R.Br. and some other smaller genera to a greatly expanded *Vincetoxicum* Wolf (Liede-Schumann & Meve 2018), and the most recent treatment of the Marsdenieae (Liede-Schumann et al. 2022), which has also led to a new classification of the tribe. For the present contribution, we thus follow the expanded concept of *Ceropegia* of Bruyns et al. (2017).

The  $\pm$  730 species of *Ceropegia* (in the broad sense, i.e., sensu Bruyns et al. 2017, 2018a, b, 2020; Rodda & Meve 2017; Bruyns 2018; Wu et al. 2019; Biju et al. 2020) are confined to the Old World, where they occur widely around the perimeter of the Indian Ocean, mostly in seasonally dry habitats. Species are found throughout much of Africa (though they are absent from the driest parts of the Sahara Desert), Macaronesia (Bruyns 1986) and Madagascar; the Arabian Peninsula (Bruyns 1989); and from Afghanistan and the Himalayas to Southeast Asia, the Philippines and Northern Australia (Forster 1996). Since Huber’s revision (1957), new information has been published in several regional revisions and certain areas have been identified where *Ceropegia* is particularly diverse. These include South Africa (Dyer 1980, 1983; Bruyns 1985), East Africa (Archer 1992; Masinde 2000; Goyder et al. 2012), the Flora Zambesiaca region mainly around the drainage system of the Zambezi River (Goyder et al. 2020), India (Ansari 1984; Kambale & Yadav 2019) and parts of Thailand (Thaithong et al. 2018).

*Ceropegia lineariloba*, figured here, belongs to sect. *Quaqua* (N.E.Br.) Bruyns, which contains 19 species and is part of the stem-succulent stapeliad lineage. Members of this section occur from southwestern Namibia throughout Namaqualand to the southern parts of the Western Cape and eastward as far as Willowmore in the Eastern Cape. Section *Quaqua* is thus restricted to the Greater Cape Floristic Region (Manning & Goldblatt 2012; Snijman 2013) in the western and southern parts of southern Africa, which receives most of its rainfall during winter months. It occurs in the drier areas in the Fynbos and Succulent Karoo biomes.

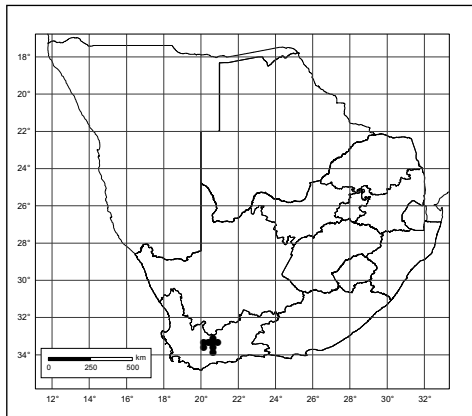


FIGURE 2.—Known distribution of *Ceropegia lineariloba*.

The first specimen of *Ceropegia lineariloba* was collected by Thomas C.J. Bain, son of road engineer Andrew Geddes Bain (Codd & Gunn 1985), in 1875 in Seweweekspoort, Western Cape. This was among a selection of stapeliads collected at the request of Sir Henry Barkly, then Governor of the Cape. Barkly regularly sent specimens to the herbarium at the Royal Botanic Gardens, Kew. On this occasion, he managed to assemble such a remarkable selection of stapeliads, that a special volume of Hooker's *Icones Plantarum* was dedicated to them (Brown 1891). *Ceropegia lineariloba* remained little-known after Bain's collection and, although it was recorded again by Joseph Archer in 1934 near Matjiesfontein, White & Sloane (1937) were unable to

add anything new to Brown's account of 1891. It was collected again in January 1976 in the mountains south of Laingsburg (Bruyns 1977). In this area it had first been noticed by Gesina Carolina du Plessis and her family, who farmed in the area and were very interested in the flora of the surrounding countryside. The known distribution is shown in Figure 2.

Originally classified as *Caralluma linearis* by Brown (1891), it was moved to the genus *Quaqua* N.E.Br., as *Quaqua linearis* (N.E.Br.) Bruyns, when *Quaqua* was resurrected (Bruyns 1983). *Quaqua* was originally created by Brown for the single species *Quaqua hottentorum* N.E.Br. and he derived this name from the local name *Gwagwa* (or *Qua-qua*) for this species and others. Because the name *Ceropegia linearis* E.Mey. already existed in *Ceropegia*, a new specific epithet had to be found for *Quaqua linearis* when it was moved to *Ceropegia*, which is why it was renamed as *C. lineariloba* (Bruyns et al. 2017).

*Ceropegia lineariloba* has unusually darkly coloured, almost black, branches, especially on new growth. Because of this trait, the local farmers and San people in its distribution area know it, and other members in sect. *Quaqua*, as *swart aroena* or *swart ouram* (Van Wyk & Gorelik 2017). The tubercles on the branches do not have the hard and sharp tips that are typical of sect. *Quaqua*, instead they are blunt or round-tipped – a feature that they share with *C. ramosa* (Masson) Bruyns. Within sect. *Quaqua* the flowers are distinctive for their slender lobes (giving rise to both the original specific epithet *linearis* and the subsequent specific epithet *lineariloba*), which are dark maroon inside and change quite abruptly near the mouth of the tube to the white colour of the tube (Figure 3).

The holotype of *Ceropegia lineariloba* is housed in the herbarium at the Royal Botanic Gardens, Kew. This specimen is a cutting of the plant found by Bain and so the original description did not include the fact that the plant is a dwarf shrub that is rarely more than 80 mm tall. Brown (1891) sketched the flowers and observed that their shape and colouration may have been distorted during preservation and transportation and, indeed, the shape of the corolla is unlike his illustration, though his representation of the corona is accurate.

The typical habitat of *Ceropegia lineariloba* is characterised by acidic soils derived from sandstones, usually of the Witteberg Series. Like *C. nevillei* Bruyns (previously *Quaqua pillansii* (N.E.Br.) Bruyns), *C. lineariloba* grows exclusively on such sandy soils, and is known to occur only on dry, rocky, north-facing slopes and flat, rocky areas with shallow soils among other shrubs (Bruyns 2005). *Ceropegia lineariloba* occurs in association with *Pteronia fastigiata* Thunb., a compact and small-leaved form of *Crassula rupestris* Thunb., *Braunsia apiculata* (Kensit) L.Bolus and others. The species has a Red List status of Least Concern (Raimondo 2009), as there are currently no threats to the known populations.

Several members of *Ceropegia* (especially among the large- and flat-flowered stapeliads) are known for their foul- or putrid-smelling flowers (Bruyns 2005). Many have other floral adaptations that mimic carrion or other decaying substances, which appear to promote pollination by flies. These adaptations include flowers that open in the late afternoon and close in the early hours of the morning, coinciding with the peak time of activity of flies (Agnew 1976). Flowers that have red and white colouration resembling flesh (Bruyns 2000), as in the case of *C. lineariloba*, or flowers with textured and hairy surfaces, as in several members of sect. *Stapelia* (L.) Bruyns. The flowers of *C. lineariloba* appear between March and mid-April and emit a weak but unpleasant, dung-like odour. While nothing is known about the pollination of *C. lineariloba*, its floral morphology clearly fits with the sapromyophilous pollination syndrome prevalent in other *Ceropegieae* (e.g., Jürgens et al. 2006; Du Plessis et al. 2018).

Although there is no information on the medicinal properties of *Ceropegia lineariloba*, data have been gathered for other members of *Ceropegia* and within the Apocynaceae. It is worth expanding on some of these, as similar ethnobotanical properties may be found in *C. lineariloba* and related taxa. Nortje (2011) mentions that *C. mammillaris* (L.) Bruyns, a relative of *C. lineariloba*, has been used as an appetite stimulant and as treatment for cancer by people in the Kamiesberg area. Its flowers and fruits are also consumed by people and

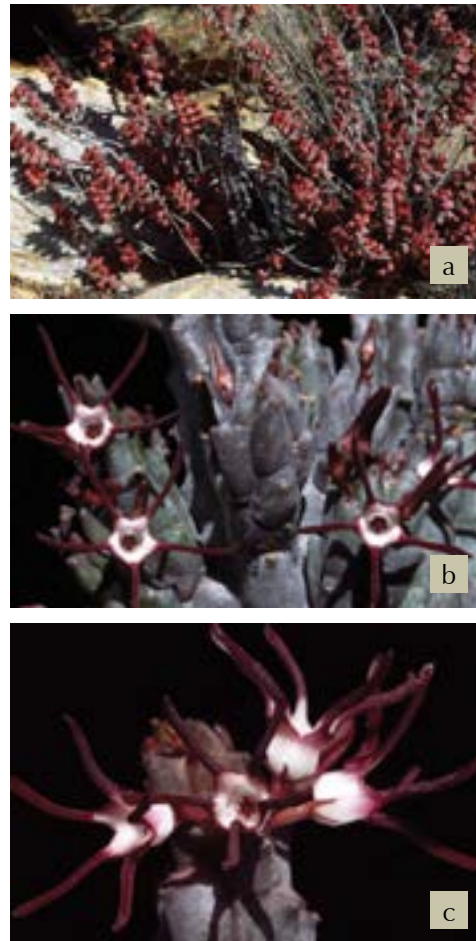


FIGURE 3.—*Ceropegia lineariloba* in habitat: a, whole plant hiding inside a small shrub of *Crassula rupestris*; b, looking straight into the flowers, bright white tube with dark lobes and corona; c, side view of flowers in a simultaneously opening cluster. Photographs: P.V. Bruyns.

are locally known as *horlosies* and *bokhorinkies* respectively (De Vynck et al. 2016). These colloquial names are generally applied to more than just one species and, for example, most species of *Microloma* are known also as *bokhorings*. *Ceropegia incarnata* (L.f.) Bruyns has also been recorded as a popular indigenous food used by people of Khoisan descent (De Beer & Van Wyk 2011). *Ceropegia incarnata* and *C. mammillaris* are both edible and their succulent branches are eaten fresh (De Beer & Van Wyk 2011). The roots of *C. candelabrum* L. and other species are widely used in Indian traditional medicine for the treatment of diarrhoea and dysentery (Beena & Martin 2003; Sri Rama Murthy et al. 2010; Karuppusamy et al. 2013). *Ceropegia cumingiana* Decne. has been used as a yam by the indigenous people of Queensland in Australia (Bruyns & Forster 1989).

*Ceropegia lineariloba* is likely to be most closely related to *C. ramosa* within sect. *Quaqua* and is also the most morphologically similar to it, e.g., both possess the unusual feature of rounded tubercles along their branches. There are several morphological differences that can be used to distinguish between them, some of which are listed in Table 1. Another

Table 1.—Comparison of three closely related *Ceropegia* species from the western parts of South Africa

| Character                | <i>Ceropegia lineariloba</i><br>(= <i>Quaqua linearis</i> )                                                                                             | <i>Ceropegia ramosa</i><br>(= <i>Quaqua ramosa</i> )                                                                                                                                                                          | <i>Ceropegia nevillei</i><br>(= <i>Quaqua pillansii</i> )                                                                                         |
|--------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------|
| <b>Stem and branches</b> | Erect, 50–200 × 10–25 mm, uniformly dark green to purple-black and darker on younger growth.                                                            | Erect, 60–300 × 15–30 mm, uniformly purplish to greyish green.                                                                                                                                                                | Erect, 150–400 × 20–40 mm, grey-green, mottled with purple-brown.                                                                                 |
| <b>Tubercles</b>         | 2–5 mm long, broadly deltoid, laterally flattened, spreading, fused into 4 obtuse angles along branch, each tipped with a minute hardened tip.          | 3–5 mm long, broadly deltoid, laterally flattened, spreading, obtuse and joined in lower half into 4 obtuse angles along branch, each tipped with a small tooth or corky, brown patch flanked by 2 obtuse stipular denticles. | 8–15 mm long, deltoid, laterally flattened, spreading, joined in lower half into 4 obtuse angles on branch, each tipped with a hard yellow tooth. |
| <b>Inflorescence</b>     | 1–6 simultaneously opening flowers, in lax fascicles mainly in upper half of branches.                                                                  | 2–15 simultaneously opening flowers, in dense fascicles in upper half of branches.                                                                                                                                            | 4–20 simultaneously opening flowers, in dense fascicles in upper half of branches.                                                                |
| <b>Sepals</b>            | 2.0–2.5 mm long, ovate-acute, pink.                                                                                                                     | 2–3 mm long, lanceolate-acute, pinkish.                                                                                                                                                                                       | 2–3 mm long, ovate-acute, speckled with purple.                                                                                                   |
| <b>Corolla</b>           | 9–22 mm long, campanulate to ± rotate, outside reddish purple on lobes becoming white towards bases of lobes.                                           | 13–15 mm long, campanulate, outside shiny purple-black on lobes to red on tube and cream at base.                                                                                                                             | 12–18 mm long, campanulate, outside shiny dark purple-brown to pale red, cream speckled with purple-red at base.                                  |
| <b>Lobes</b>             | 8–14 mm long, 2–4 mm broad at bases, erect to spreading, linear, longitudinally strongly folded back along middle so that most of lobe only 1 mm broad. | 7.5–12.0 mm long, 3.5–4.0 mm broad at bases, erect to spreading, narrowly lanceolate, longitudinally folded back along middle.                                                                                                | 7–11 mm long, 4–6 mm broad at bases, erect to spreading, oblong-ovate, longitudinally slightly folded back along middle.                          |

species that is also known to grow on sandstone-derived substrates, namely *C. nevillei*, has been included in this table for further comparison. Of these three, *C. nevillei* has the widest distribution, overlapping with other species (Bruyns 2005).

**Description.**—A small succulent that grows up to 200 × 150 mm, rooting only on the central stem, branching mainly above base. *Branches* 50–200 × 10–25 mm, erect, uniformly dark green to purple-black, with particularly dark colouration on younger growth; tubercles 2–5 mm long, broadly deltoid, laterally flattened, with spreading habit, joined into 4 obtuse angles along branch, each tipped with small hardened deltoid tooth, mostly less than 1 mm long and flanked by 2 very small stipular denticles. *Inflorescence* 1–6 simultaneously opening flowers, borne in lax fascicles mainly in upper parts of branch; pedicel 1–7(–10) × 1.5 mm, spreading and holding the flower horizontally facing. *Sepals* 2.0–2.5 mm long, ovate-acute. *Corolla* 12–18 × 9–22 mm, campanulate to ± rotate; tube 3–4 mm long, 5 mm broad at mouth, cupular, corolla very slightly thickened at mouth; lobes 8–14 mm long, 2–4 mm broad at bases, erect to spreading, strongly folded back longitudinally along middle so that most of the lobe is only 1 mm broad, often widening again slightly before becoming abruptly acute and slightly incurved at apex, red-purple outside becoming white towards base and dark red-purple above, glabrous and smooth. *Corona* ± 2.5 × 2.2–2.8 mm, with purple colouration on lobes becoming white towards the base, raised on a very short stipe; outer lobes ± 1 mm long, erect, shortly bifid into more or less erect, deltoid obtuse lobules, sometimes with denticles between them, fused laterally in the lower half to the bases of the inner lobes to form a deep pouch; inner lobes 2 mm long, adpressed to the backs of the anthers then rising in a column above the centre and curving back outwards, linear, obtuse, dorsiventrally flattened and without dorsal projections. *Fruit* 80–100 mm long, purple-black. *Seeds* narrowly oblong, with a thick roll-like margin, short coma with hairs ± 12 mm long. Plate 2396.

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PLATE 2397 *Lobostemon belliformis*

*Lobostemon belliformis*

Boraginaceae

South Africa

***Lobostemon belliformis*** Buys in South African Journal of Botany 62,1: 31 (1996); Buys: 79 (2011).

*Lobostemon belliformis* is a member of the Boraginaceae, commonly referred to as the forget-me-not or borage family. Species in the family are globally distributed in tropical, subtropical or temperate areas and are annual or perennial herbs (particularly in the Mediterranean region), shrubs, woody climbers or large trees (Heywood et al. 2007). Plants in this family are characterised by distinctive rough hairs on their leaves, an inflorescence that usually coils at the tips, stamens that are attached to the petals and fruits, although formed from two locules, often present as four nutlets by means of false septa. Despite these shared characteristics, taxa traditionally placed in the Boraginaceae have varying morphologies with consensus regarding the circumscription of the family rather elusive. In 2016, Luebert et al. promoted a restricted circumscription of the Boraginaceae and Chacón et al. (2016) recognised three subfamilies consisting of  $\pm$  90 genera with 1 600–1 700 species. The Boraginaceae is widely distributed within southern Africa, with members present in the Fynbos, Desert, Savanna, Succulent Karoo, Nama-Karoo and Thicket biomes (Mucina & Rutherford 2007).

*Lobostemon*, currently with 28 species (Buys 2011), is the largest genus of the southern African Boraginaceae. It is endemic to South Africa, occurring primarily in the Greater Cape Floristic Region (Born et al. 2007). The first species of *Lobostemon*, described by Linnaeus (1753) from the Cape of Good Hope, was initially placed in *Echium* L., namely *E. fruticosum* L. In subsequent years, numerous additional South African *Echium* species were described before Lehmann (1830) described *Lobostemon* for *L. echioides* Lehm. As the main distinguishing generic character, Lehmann stressed the presence of staminal scales (Buys 2006). Indeed, the generic name is in reference to these scales with both Latin and Greek origins – the Latin *lobos* (meaning ‘lobe’) and the Greek *stemon* (meaning ‘stamen’). Buek (1837) extended Lehmann’s concept of *Lobostemon* to include taxa that have reduced staminal scales or no staminal scales at all, but instead slightly thickened staminal bases. Consequently, Buek (1837) transferred a number of *Echium* species from South Africa to *Lobostemon*, thereby confining *Echium* to Western Eurasia. The next century saw the South African taxa being moved back and forth between *Lobostemon* and *Echium*; for a detailed discussion of this period, see Buys (2011).

Taxonomic stability returned when Levyns (1934) revised *Lobostemon* and recognised *Echium* as a separate genus, though closely related. This view has been verified by morphological data (Buys 2006) and DNA analyses (Böhle et al. 1996; Chacón et al. 2019; Hilger

& Böhle 2000). Levyns (1934) delimited five sections within *Lobostemon*, mainly based on floral morphology. *Lobostemon* section *Grandiflori*, which is important for the context of our species under discussion, is characterised by species with regular tubular corollas, highly reduced staminal scales and stamens of equal length. Levyns (1934) assigned *L. montanus* H.Buek, *L. sanguineus* Schltr. and *L. regulariflorus* (Ker Gawl.) Buys (= *L. grandiflorus* (Andrews) Levyns) to this section. Buys & Van der Walt (1996) remarked with the description of *L. belliformis* that it is similar to *L. regulariflorus* in terms of, for example, leaf shape, corolla colour (to some degree), flower size (corolla tubes  $\pm$  44–47 mm long), reduced staminal scales and a glabrous inter-scale area. Yet, there are differences: *L. belliformis* has a bell-shaped corolla tube, whereas *L. regulariflorus* has a corolla tube that widens uniformly (tubular); *L. belliformis* has leaves with revolute margins and indumentum occurs on both surfaces, whereas *L. regulariflorus* has flat leaf margins and the indumentum occurs only on the adaxial surface (Buys 2005). Subsequent to the description of *L. belliformis* and the placement of it in *Lobostemon* section *Grandiflori*, Buys (2006) showed that *Lobostemon* section *Grandiflori* could no longer be justified from an evolutionary perspective and combined it with *Lobostemon* section *Fruticosi*, hypothesising that *L. regulariflorus* and *L. belliformis* are sister taxa. One possible explanation is that convergent evolution, in response to bird pollinators, may explain the similarity between the two mentioned species' floral characters (Buys & Van der Walt 1996). Intriguingly, unpublished molecular sequence data generated by the Royal Botanic Gardens, Kew, does not group *L. regulariflorus* and *L. belliformis* (P. Malakasi & F. Forest, personal communications). Another red-flowered species is *L. sanguineus* and the key below will assist fieldworkers in identifying the three red-flowered species of *Lobostemon* (Figure 1).

### Key to the red-flowered *Lobostemon* species

- 1a. Leaves coriaceous; mature flowers shorter than 35 mm; staminal scales well developed, area between staminal scales pubescent . . . . . *L. sanguineus*
- 1b. Leaves herbaceous; mature flowers longer than 35 mm; staminal scales reduced to swellings, area between staminal scales glabrous . . . . . 2
- 2a. Leaves adaxially and abaxially hairy, leaf margins revolute; flowers varying from white to salmon pink to red, bell-shaped, with red to maroon nectar guides (especially prominent in lighter coloured flowers). . . . . *L. belliformis*
- 2b. Leaves adaxially hairy, abaxially glabrous, leaf margins not revolute; flowers red, tubular, red nectar guides not prominent . . . . . *L. regulariflorus*

A total of five collections (including the type specimen) were available for study by Buys (2011) – indicative of the rarity of the species. From a conservation perspective, Hilton-Taylor (1996) regarded the species' status as Endangered. Upon reassessment, the status was increased to Critically Endangered (Vlok et al. 2005) with the primary threats identified as habitat degradation, mainly due to invasive alien species, and harvesting. *Lobostemon belliformis* is a slow-growing species that can become very old, the generation time is thought to be 40 years (Vlok et al. 2009). Until recently, the species was only found on stabilised sand dunes associated with Canca Limestone Fynbos (Mucina & Rutherford 2007) near Gourikwa (Figure 2). Turner (2018) reports the remarkable discovery of a new population of *L. belliformis* by the Outramps branch of the Custodians of Rare and Endangered Wildflowers (CREW). The new locality is 200 km to the east of Gourikwa in the vicinity of Spioenkop, Sedgelyfield (Figure 2), which is associated with Knysna Sand Fynbos (Mucina & Rutherford 2007).



FIGURE 1.—The three red-flowered species of *Lobostemon*: a, *L. sanguineus* with erect, funnel-shaped to shortly tubular flowers and erect corolla lobes; b, *L. belliformis* with bell-shaped flowers and spreading corolla lobes; c, *L. regulariflorus* with tubular flowers and spreading to semi-erect corolla lobes. Photographs: a, G. Malan (CC BY-NC) with permission from iNaturalist; b, c, M.H. Buys.

Most species of *Lobostemon* are difficult to grow from stem cuttings because the cuttings do not root well (Buys & Van der Walt 1996; Lodama et al. 2016; Swarts et al. 2018), which only makes conservation efforts more difficult. It is, therefore, heartening that seedlings of *L. belliformis* have been observed (iNaturalist 2020). Fire is an important factor for all plant species within the Fynbos Biome. *Lobostemon belliformis* escapes fire by growing on rocky outcrops and they also possess very thick bark for some protection (Vlok et al. 2009). The plants can grow from seedbanks or resprout after a fire event, if the seeds or plants are not too severely damaged.

*Lobostemon belliformis* (Figure 3), like *L. regulariflorus*, has striking flowers that conform to a floral syndrome associated with bird pollination (ornithophily). Red flowers have been found to be both attractive for birds and repellent for insects (Cronk & Ojeda 2008). In contrast to *L. regulariflorus*, where the flowers are, as far as is known, uniformly red, the flowers of *L. belliformis* vary from entirely red, to salmon pink, to a mixture of white and

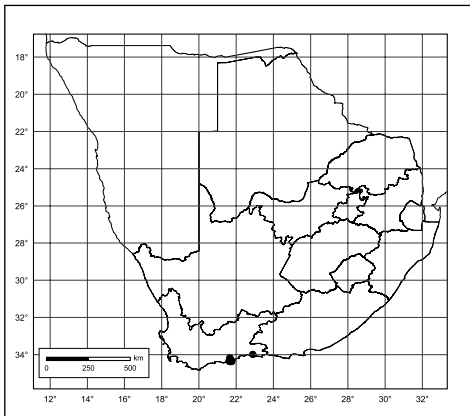


FIGURE 2.—Known distribution of *Lobostemon belliformis*.

pink or red, to almost entirely white. Flowers all possess red to maroon nectar guides visible on both surfaces of the corolla tube. Additional insect exclusion mechanisms present in *L. belliformis* and *L. regulariflorus* are their pendent flowers that do not present a landing platform for insects, coupled with a long corolla tube. The sterile and robust peduncles provide secondary perches for visiting birds in both species and the corolla lobes are the most rigid in the genus to counter any damage visiting birds may cause. In addition, dense floral clustering enables birds to probe several flowers from the same perch. Buys & Van der Walt (1996) observed the Southern



FIGURE 3.—*Lobostemon belliformis* characters: a, leaves with revolute margins and salmon pink flowers; b, white flowers with prominent nectar guides; c, red flowers; d, almost regular flowers with spreading corolla lobes. Photographs with permission from iNaturalist: a, Sandra Falanga (CC-BY-NC); b, Dave Underwood (CC-BY-NC); c, d, Nicola van Berkel (CC BY-SA).

Double-collared (*Cinnyris chalybeus*) and Orange-breasted sunbirds (*Anthobaphes violacea*), and the Cape Sugarbird (*Promerops cafer*) visiting *L. belliformis*. The pollination biology of *L. belliformis* is worthwhile investigating further to confirm ornithophily and to determine the purpose of the nectar guides.

The rarity and remoteness of *Lobostemon belliformis* explains the absence of any recorded details of any potential medicinal purposes. The common name, beaut health-bush, as per iNaturalist (2020), implies healing properties. The association of any species of *Lobostemon* with medical plants is mainly due to *L. fruticosus* (L.) H.Buek (1837) – known colloquially as *agtdaegeneesbos* (eight-day-healing-bush) – which has been used for the treatment of various ailments, especially those concerning wounds, blood poisoning, ring-worms, skin diseases and syphilis. The remedies all require an infusion of the leaves or a paste made from either pounding or chewing the leaves (Watt & Breyer-Brandwijk 1962; Van Wyk et al. 1997; Philander 2011; Van Vuuren & Frank 2020). The Boraginaceae are, however, a common source of pyrrolizidine alkaloids that act as cumulative liver toxins and the use of substances containing them is discouraged (Bruneton 1999).

The species name is descriptive of the flowers and is derived from the Latin words *bella/bellis* (meaning ‘beautiful’) and *formis* (meaning ‘form’). The specimen used as a voucher for the accompanying plate was cultivated at Kirstenbosch National Botanical Garden and was originally sourced from the Gourikwa site.

**Description.**—Woody shrub, 1.0–1.5 m high. *Branches* alternate, antrorse, young branches hairy becoming hairless with age; cork thick. *Leaves* herbaceous, sessile, oblanceolate, (50–)60–90(–100) × (5–)8–12(–15) mm, apex acuminate, margins revolute, mid-vein prominent on the abaxial surface, adaxially and abaxially hairy, hairs similar in length; stipules absent. *Inflorescence* of many flowered, compound cincinni, young flowering axis compact, flower buds loosely arranged, axis spreading slightly in fruiting stage. *Bracts* lanceolate, adaxially and abaxially hairy. *Flowers* more than 3 per cymule, corolla tubular, bell-shaped. *Sepals* narrowly oblong, half of corolla length, dissimilar in width, 2–4 sepals partly fused, adaxially and abaxially copiously hairy, young apices flat. *Corolla* ± 44–45 mm long, white to salmon pink to red, nectar guides red to maroon and particularly visible in white to salmon pink flowers, abaxially hairy, corolla lobes ± 6–7 mm long, spreading. *Stamens* straight, slightly dissimilar in length, included to exerted in adult flowers; anthers dorsifixed; filaments long adnate (> 5 mm) above staminal scales; staminal scales inserted well below the throat of the corolla tube, 3 mm above the base of the corolla tube, reduced to mere swellings, lateral lobes absent, villous, area between scales glabrous. *Gynoecium* 2-carpelled; ovary superior, 4-locular (via false septa); nectariferous disc present; style median sections hairy. *Fruit* smooth, ovoid-trigonous mericarpids (nutlets). *Flowering time*: late June to September. Plate 2397.

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*Barleria lancifolia* subsp. *lancifolia*

Acanthaceae

*Namibia, Botswana, Zimbabwe, Eswatini, Mozambique and South Africa*

**Barleria lancifolia** T.Anderson in Journal of the Linnean Society, Botany 7: 28 (1864); Moore: 404 (1902); Moore: 230 (1907); Obermeyer: 147 (1933), excl. *B. alata* S.Moore; Meyer: 381 (1957); Meyer: 15 (1968), pro maj. parte; Balkwill & Balkwill: fig. 2H, 7D, 12M & R (1997); Darbyshire: 101 (2015); Darbyshire et al.: 152 (2021). *Barleria hereroensis* Engl.: 261 (1888). *Barleria latiloba* Engl.: 261 (1888). *Barleria cinereicaulis* N.E.Br. ex C.B.Clarke: 53 (1901). *Barleria rautanenii* Schinz: 437 (1916). *Barleria alata* sensu Clarke: 158 (1899), pro parte, non S.Moore: 266 (1880).

*Barleria* L. is a large and diverse genus in the family Acanthaceae Juss., nom. cons. Acanthaceae are one of the largest flowering plant families with 191 genera and an estimated 4 900 species worldwide (Manzitto-Tripp et al. 2022) and is represented by 40 genera and  $\pm$  375 species in southern Africa (SANBI 2022). Members of the family are mostly represented by annual and perennial herbs, shrubs and climbers, with relatively few trees (Darbyshire & Luke 2016), although these include some important mangrove species (Schwarzbach & McDade 2002). The highest diversity of members of the family within southern Africa is found in the northeastern parts of the region with relatively high summer rainfall and it is comparatively low in winter-rainfall areas (SANBI 2022). According to Balkwill et al. (2021: 194), ‘some groups of the family predominate in the moister eastern areas and have capsules that open upon drying, whereas others dominate in the drier western areas and have capsules that open upon wetting.’

The Acanthaceae family is an ecologically important group of plants in sub-Saharan Africa (Kroon 1999; Vollesen 2000; Wahlberg 2001; Darbyshire et al. 2020). They are also of economic importance as fodder for livestock and wildlife (Vollesen 2000; Mannheimer et al. 2008; Tripp et al. 2017; Darbyshire et al. 2019a), as ornamental plants with showy flowers or bracts, and as medicinal plants (Watt & Breyer-Brandwijk 1962; Van Wyk & Gericke 2000). The leaves, containing compounds with anti-fungal, cytotoxic, anti-inflammatory, insecticidal or anti-viral activity (Van Wyk & Gericke 2000; Awan et al. 2014; Lekhak et al. 2022), are mainly used medicinally.

The tribe Barlerieae of subfamily Acanthoideae (McDade et al. 2008; Manzitto-Tripp et al. 2022) comprises 13 genera and approximately 500 species, with three genera occurring in the Flora of southern Africa (FSA) region, namely *Barleria*, *Crabbea* Harv. and *Lepidagathis* Willd. (Darbyshire et al. 2019a; SANBI 2022), and can be distinguished from other Acanthaceae by quincuncial corolla aestivation – two petals exterior, two interior and the fifth with one margin interior and the other exterior (Figure 1) (Darbyshire et al. 2019b; Manzitto-Tripp et al. 2022).

PLATE 2398.—1, flowering branch,  $\times$  1; 2, opened corolla,  $\times$  1; 3 bracteoles,  $\times$  2; 4, outer calyx lobes,  $\times$  2; 5, lateral calyx lobes,  $\times$  2; 6, dehiscent capsule,  $\times$  2. Voucher specimens: 1, 2, *Condy 385*; 3–6, *Condy 386* in National Herbarium (PRE), Pretoria. Artist: Gillian Condy.



PLATE 2398 *Barleria lancifolia* subsp. *lancifolia*



*Barleria* comprises  $\pm$  300 accepted species (Darbyshire 2019a, b) and is mainly found in the warmer parts of Africa and Asia. Eight centres of endemism have been recognised in Africa, including Madagascar (Balkwill & Balkwill 1998; Darbyshire et al. 2019a), with remarkably high rates of local endemism (Darbyshire & Luke 2016; Darbyshire et al. 2019a). For example, in Namibia and Angola 75% of the taxa are endemic to the area. A similar rate of endemism is true for other parts of its range, e.g., in Tanzania. Endemism is over 90% on Madagascar (Darbyshire et al. 2021). The genus is well represented in southern Africa, by  $\pm$  74 taxa (SANBI 2022). New species of *Barleria* continue to be described from this region, most recently two species in subg. *Barleria* were described from the Soutpansberg of Limpopo Province (Darbyshire et al. 2022).

Many characters in *Barleria* are highly variable, but the genus is defined by a combination of the following: the presence of a four-lobed calyx consisting of two outer and two inner segments; spheroidal, honey-combed pollen; a predominance of double cystoliths in the leaves; quincuncial corolla aestivation (Figure 1); and a corolla that is not clearly two-lipped and without a hooded dorsal lip (Balkwill & Balkwill 1997; McDade et al. 2008; Darbyshire 2015, Darbyshire et al. 2019b). In most (or possibly all) species, the two abaxial stamens twist and cross towards the base, a character that is potentially unique to this genus (Darbyshire et al. 2019b).

Recent treatments of *Barleria* (Darbyshire et al. 2019a, b, 2021; Comito et al. 2022) divide the genus into two subgenera, namely *Barleria* and *Prionitis* as proposed by Balkwill & Balkwill (1997), with the modification that sect. *Fissimura* is now treated in subgenus *Barleria*. Subgenus *Prionitis* is divided into three sections (*Prionitis*, *Somalia* and *Stellatohirta*), mainly based on the absence or presence of spines, and the indumentum, corolla and capsule characters (Darbyshire et al. 2019a, b). Subgenus *Barleria* is characterised by unbeaked, two- or four-seeded capsules; if capsules are two-seeded, then the hairs are not star-shaped or tree-like, the corolla tube is salver-shaped (with a slender tube and an abruptly widening limb) and the stigma is head-like or club-shaped. Subgenus *Prionitis* predominantly has two-seeded capsules, with a prominent beak (except in some members of sect. *Stellatohirta*); if capsules are two-seeded and lack a prominent beak, then the indumentum is star-shaped or tree-like, the corolla tube is cylindrical and the stigma is linear (Darbyshire et al. 2019a, b). For more information on the history of infrageneric classification and taxonomic studies

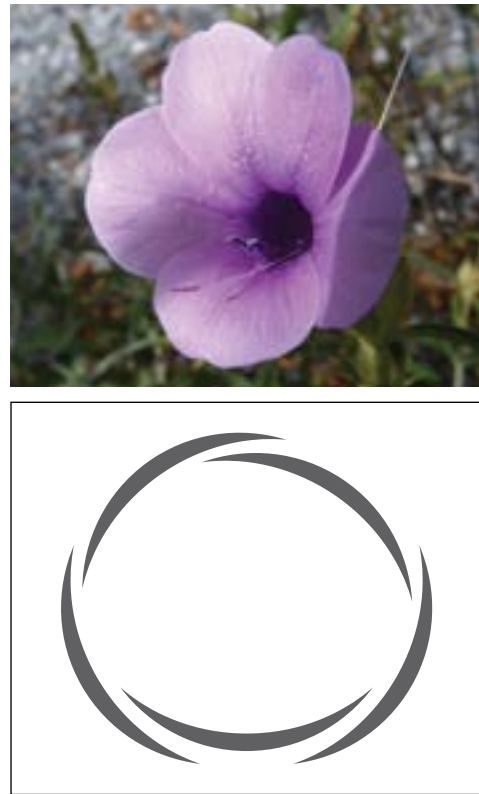
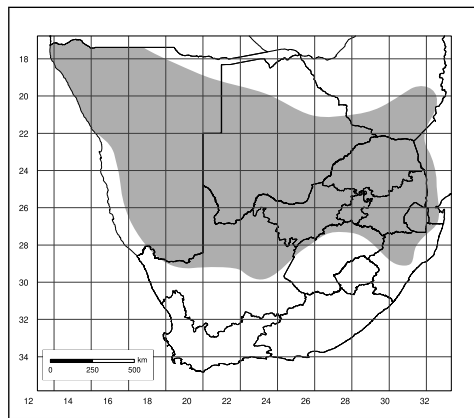


FIGURE 1.—Diagram and photograph showing quincuncial corolla aestivation. Photograph: E. Manzitto-Tripp.

TABLE 1.—Comparison of characters used to distinguish between *Barleria lancifolia*, *B. grootbergensis* and *B. mackenii* (adapted from Darbyshire et al. 2021)

| Characters                                         | <i>Barleria lancifolia</i>                                          | <i>Barleria grootbergensis</i>        | <i>Barleria mackenii</i>                                      |
|----------------------------------------------------|---------------------------------------------------------------------|---------------------------------------|---------------------------------------------------------------|
| <b>Inflorescences</b>                              | Axillary cymes or lax spikes.                                       | Dense, terminal spikes.               | Axillary, 1–3-flowered.                                       |
| <b>Indumentum (stems, bracteoles, calyx lobes)</b> | Densely glandular pubescent.                                        | Densely glandular pubescent.          | Glandular hairs lacking.                                      |
| <b>Anterior (outer) calyx lobe – shape</b>         | Elliptic or ovate.                                                  | Elliptic or subrhombic.               | Broadly ovate.                                                |
| <b>Anterior (outer) calyx lobe – base</b>          | Cuneate or acute.                                                   | Cuneate or attenuate.                 | Subcordate.                                                   |
| <b>Anterior (outer) calyx lobe – size in fruit</b> | 12.5–20.0 × 9.5–13.5 mm                                             | 11–19 × 5.5–9.0 mm                    | 19–32 × 18–25 mm                                              |
| <b>Corolla tube</b>                                | Funnel-shaped or narrowly so.                                       | Subcylindrical or gradually expanded. | Cylindrical, then abruptly funnel-shaped.                     |
| <b>Abaxial corolla lobe offset</b>                 | 3.5–7.0 mm                                                          | 5–9 mm                                | 1.5–4.5 mm                                                    |
| <b>Distribution</b>                                | Namibia, Botswana, Zimbabwe, Eswatini, Mozambique and South Africa. | Endemic to northwest Namibia.         | Angola, Namibia, Zambia, Zimbabwe, Botswana and South Africa. |

FIGURE 2.—Known distribution of *Barleria lancifolia* according to GBIF (2022) with additional localities from the C.E. Moss Herbarium, Johannesburg.

on *Barleria*, the reader is referred to Balkwill & Balkwill (1997), Darbyshire et al. (2019a, b), Balkwill et al. (2021) and Comito et al. (2022).

*Barleria lancifolia* falls within subgenus *Prionitis*, sect. *Somalia*, which is distinguished by plants being unarmed, glabrous or with simple and/or two-branched hairs, two or three staminodes, and a beaked capsule in which the septum has a membranous portion above the retinacula (Darbyshire et al. 2019b, 2021). This species is distinguished from closely related species, namely *B. grootbergensis* I.Darbysh. and *B. mackenii* Hook.f., mainly based on inflorescence and flower characteristics, as well as their distribution (Table 1).

The specific epithet *lancifolia* refers to the leaf shape of this species and means lance-shaped leaves. *Barleria lancifolia* is assessed and Red-Listed as LC (Least Concern), as it is a widespread species (Figure 2) often being abundant in a range of habitats, including rocky hillslopes and deserts (Darbyshire et al. 2021). It also occurs in areas of low agricultural



FIGURE 3.—*Barleria lancifolia*: a, in habitat; b, outer calyx lobes showing glandular hairs; c, d, close-ups of flower. Photographs: D. Smith.

value, is tolerant of some disturbance and is often found along roadsides (Darbyshire et al. 2021). *Barleria lancifolia* grows at altitudes of 460–2 100 m in a range of vegetation types. It is mostly restricted to Nama-Karoo, Savanna and Grassland biomes. *Barleria lancifolia* mainly flowers from late summer to early winter (February to June) (SANBI 2022) and the flowers are blue, mauve to lilac with a paler tube and the mouth either darker purple or white (Darbyshire et al. 2021) (Figure 3).

9. *B. LANCIFOLIA*, T. Anders. Erecta, pruinosa; foliis lineari-lanceolatis, acutis, integerrimis, mucronulatis; floribus sessilibus, axillaribus, solitariis; bracteis herbaceis, erectis, linearibus, calyce dimidio brevioribus; calycis laciniis herbaceis, integris, glandulosis, exterioribus ovatis vel ovato-lanceolatis, acutis, interioribus brevioribus, lanceolatis corolla infundibuliformi, tubo brevissimo, fauce dilatata, lobis late ovato-rotundatis; staminibus fertilibus 2, inclusis, filamentis basi connatis, anantheris 3 brevissimis; ovulis 4; capsula rostrata, glanduloso-tomentosa.

*Hab.* In Damara Land, regione Africae austro-occidentalis, in herb. Coll. Trin. Dubl.

*Suffrutes* parvus. *Caulis* teres, cortice cinereo, pruinoso. *Folia* 1-2 unc. longa, juniora puberulo-glandulosa. *Bractea* 3 lin. longae, angustissime lineares. *Calycis* lacinae exteriores 3-6 lin. longae. *Corolla* 1½ unc. longa, pulchra, limbo amplo, lobis patentibus.

FIGURE 4.—Protologue of *Barleria lancifolia* (Anderson 1864: 28).

The type specimen of *Barleria lancifolia* was collected by an unknown collector, as there is no record of Anderson visiting South Africa or Namibia. In his protologue Anderson (1864) mentioned no date, collector or other information, just the locality (Figure 4). The type locality is Damaraland (currently in Namibia), although the label says ‘Cape of Good Hope’ (usually referring to South Africa) and is housed in the Trinity College Herbarium (TCD) (Figure 5). The oldest specimen of *B. lancifolia* in a SANBI herbarium was collected by J. Medley-Wood during April 1901 near Greytown, Natal (now KwaZulu-Natal), one of only a few specimens known from KwaZulu-Natal.

*Barleria lancifolia* can be grown from seed or cuttings and is suitable to plant in sunny areas of a garden. It can withstand drought and mild frost (Froneman 2010). No specific medicinal uses of *B. lancifolia* could be found in the literature.

*Barleria lancifolia* is a variable species and more than one taxon may be involved in the current circumscription. Four distinct forms are known from Namibia (Darbyshire et al. 2021). The specimen illustrated here was collected from Tswalu Kalahari Reserve, a private nature reserve to the northwest of Hotazel, Northern Cape, during March 2022.

A second taxon, *Barleria lancifolia* subsp. *charlesii* (Benoist) J.-P. Lebrun & Monod, has been described from Mauritania in the Sahel region of northwest Africa. It differs from the southern African material in having glabrous capsules and in lacking glandular hairs on the calyces (these usually present in *B. lancifolia* subsp. *lancifolia*). Given their extreme range disjunction, these two taxa may be better treated as separate species, although the morphological similarity is striking. If re-elevated to species status, the name *B. bonifacei* Benoist should be applied to subsp. *charlesii*. The geographical information and description provided in the present account refer only to subsp. *lancifolia*.



FIGURE 5.—Type specimen of *Barleria lancifolia* housed in Trinity College Herbarium, Dublin.

**Description** (based on Darbyshire et al. 2021).—Perennial herb or subshrub, 0.2–1.5 m tall, woody towards base; branches varying from prostrate to erect; lower stems densely and minutely white velutinous, uppermost internodes with spreading glandular hairs. Leaves petiolate, lanceolate, narrowly elliptic or ovate, 18–115 × 7–38 mm, base attenuate or cuneate, apex usually acute, apiculate, surfaces soon glabrescent except margin and midrib beneath sparsely strigulose; petiole 15 mm long; lateral veins 4–5 pairs. Inflorescences 1–3-flowered axillary cymes in upper portion of branches; cymes sessile or peduncle to 10(–25) mm long; bracts foliaceous but often much-reduced at upper nodes where typically linear or oblanceolate, 11–20 × 2–5 mm, often with scattered glandular hairs; bracteoles linear, oblanceolate or narrowly elliptic-lanceolate, 6.0–20.5 × 0.5–3.5 mm, spreading glandular pubescent, veins strigulose; flowers sessile or pedicels to 4.5 mm long. Calyx weakly accrescent; outer lobes equal, elliptic to ovate-elliptic, 7–20 × 4.0–9.5 mm in flower, 12.5–

25.0 × 9.5–13.5 mm in fruit, base cuneate or acute, apex rounded to subattenuate, apex of anterior lobe often minutely notched, external surfaces ± densely spreading glandular-pubescent, main veins strigulose, inner surface puberulous, venation prominent; lateral lobes lanceolate, 5.0–9.5 mm long in flower, 9–13 mm long in fruit. *Corolla* 26.5–48.0 mm long, blue, mauve or lilac with paler tube, mouth either darker purple or white, whole flower rarely whitish at anthesis, lateral lobes pubescent externally, elsewhere glabrous; tube funnel-shaped to narrowly so or almost cylindrical throughout, 13.0–18.5 mm long, basal cylindrical portion 3.5–4.5 mm wide, then rapidly to gradually widening to 4–12 mm at the throat; limb in '4+1' arrangement; abaxial lobe offset by 3.5–7.0 mm, obovate, 12.0–18.5 × 7.5–15.0 mm; lateral lobes obovate to elliptic 10–16 × 7.5–14.0 mm; adaxial lobes as lateral lobes but 6–10 mm wide. Stamens attached 4–5 mm from base of corolla; filaments 16.5–25.0 mm long; anthers 3.0–4.5 mm long; lateral staminodes 0.7–1.3 mm long. Ovary densely puberulous in distal half; style glabrous; stigma 1.5–2.5 mm long. *Flowering time*: February to June. *Capsule* 2-seeded, 14.0–17.5 mm long, puberulous mainly on beak or sometimes with only antrorse-glandular hairs; seeds ± 6.5 × 5 mm. Plate 2398.

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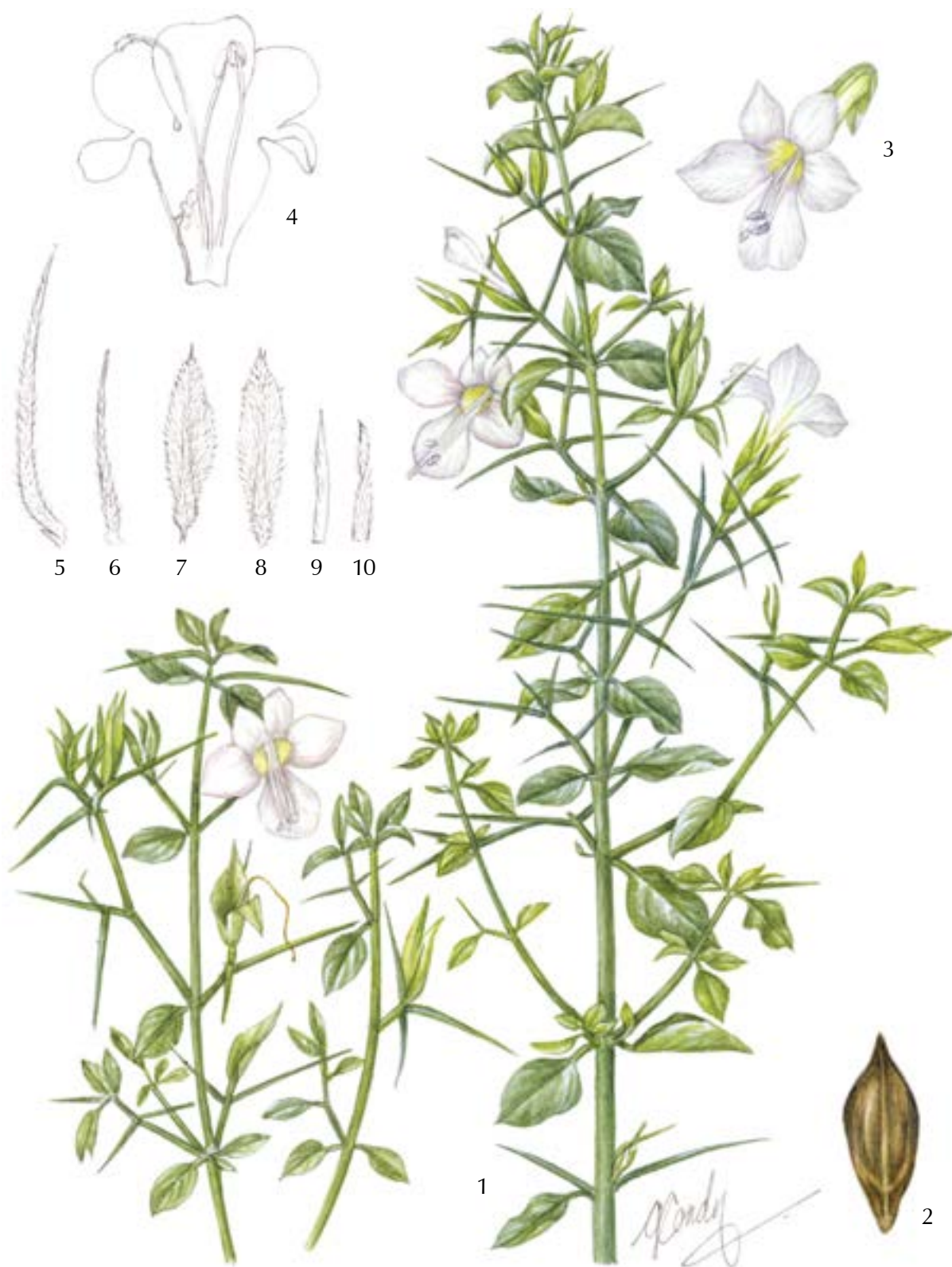


PLATE 2399 *Barleria makgabengensis*

*Barleria makgabengensis*

Acanthaceae

South Africa

***Barleria makgabengensis*** Froneman & K.Balkwill sp. nov. differs from *B. spinosissima* L. Darbysh. & K.Balkwill by having longer petioles (up to 8 mm long versus subsessile or up to 1.7 mm long); a blade on the bracteole (versus reduced to a spine); longer (16–18 mm versus 9.7–14.5 mm long) and narrower (1–2 mm versus 2.0–3.7 mm wide) anterior calyx lobes; no or light stripes in the corolla throat; and larger upper corolla lobes ( $6\text{--}7 \times 4.5\text{--}5.5$  mm versus  $3.2\text{--}5.5 \times 2.4\text{--}4.0$  mm).

TYPE.—SOUTH AFRICA, Limpopo: Senwabarwana (Bochum) District, Makgabeng, northern section, about 1 km southwest of Masebe, 1057 m (2328BD), 18 May 2022, *Balkwill & Froneman 14571* (J, holotype; E, K, MO, PRE, isotypes).

The family Acanthaceae includes an estimated 4 900 species and 191 genera (Manzitto-Tripp et al. 2021) and is vegetatively and florally very diverse (Schwarzbach & McDade 2002; Balkwill et al. 2021). Members of the family display a wide diversity in pollen morphology (Scotland & Vollesen 2000) and this character has been used in their classification. In southern Africa, members occupy a variety of habitats – some species grow in very dry conditions (Munday 1995), while others occur in moist forests (Balkwill et al. 1996).

*Barleria* L. was described by Linnaeus (1753) and commemorates Jacques Barrelier, a Dominican monk and French botanist. The genus includes over 300 species (Darbyshire et al. 2019b) of which at least 60 occur in southern Africa (Darbyshire et al. 2019a). Characters used to distinguish species and species groups (or clades) include growth form, derivation of spines, inflorescence morphology, shape and spininess of bracteoles, calyx morphology, corolla morphology, number of stamens and staminodes, presence or absence of a beak on the capsule and number of seeds (Balkwill & Balkwill 1997; Darbyshire 2009; Comito et al. 2022).

*Barleria makgabengensis* (Figure 1a) is most similar to the recently described *B. spinosissima* (Darbyshire et al. 2022), but grows as a diffuse suffrutex or climber to two or more metres tall; whereas *B. spinosissima* grows as a very dense suffrutex to small shrub up to 1 m tall (Table 1). In some plants of *B. spinosissima* the stems and leaves do not protrude beyond the mass of spines (Figure 1b); *B. makgabengensis* is never that spiny. Bracteoles in *B. makgabengensis* have a blade, are up to 19 mm long, start out green and turn straw brown; but in *B. spinosissima* they have no blade, are up to 17.5 mm long, start out purplish and turn reddish brown. Calyx lobes are longer and narrower in *B. makgabengensis*: anterior lobes  $16\text{--}18 \times 1\text{--}2$  mm (compared to  $9.7\text{--}14.5 \times 2.00\text{--}2.37$  mm in *B. spinosissima*) and posterior lobes  $17\text{--}20 \times 1\text{--}2$  mm (compared to  $10.2\text{--}17.5 \times 2.0\text{--}3.5$  mm in *B. spinosissima*). *Barleria makgabengensis* has a yellow throat, sometimes with pale lilac stripes (Figure 2a), whereas *B. spinosissima* has a yellow throat with purple lines (Figure 2b), and *B. makgabengensis*

PLATE 2399.—1, habit,  $\times 1$ ; 2, capsule,  $\times 2$ ; 3, flower,  $\times 1$ ; 4, opened flower,  $\times 2$ ; 5, 6, bracteoles,  $\times 2$ ; 7, posticous outer calyx lobe,  $\times 2$ ; 8, anticus calyx lobe,  $\times 2$ ; 9, 10, lateral calyx lobes,  $\times 2$ . Voucher specimen: *Froneman & Balkwill 1314* in National Herbarium (PRE), Pretoria. Artist: Gillian Condy.



FIGURE 1.—Comparison of flowers: a, *Barleria makgabengensis* in Makgabeng area, note larger upper corolla lobes and faint lilac stripes in throat; b, *B. spinosissima* in Van Collers Pass, Soutpansberg. Photographs: a, W. Froneman; b, K. Balkwill.

has larger upper corolla lobes  $6\text{--}7 \times 4.5\text{--}5.5$  mm (compared to  $3.2\text{--}5.5 \times 2.4\text{--}4.0$  mm in *B. spinosissima*). *Barleria bremekampii* Oberm. differs from both species by having stouter spines that have dominant eglandular hairs (rather than dominant gland-tipped hairs) and smaller upper corolla lobes. In addition, the inflorescence axis of *B. bremekampii* is reduced between nodes, making a much more compact inflorescence.

We were made aware of this taxon when Barbara Turpin sent us photographs in early May 2021. Barbara, Lize von Staden and Bronwyn Egan were part of the Limpopo branch

Table 1.—Summary of differences between *Barleria spinosissima* and *B. makgabengensis*

| Character                   | <i>B. spinosissima</i>                         | <i>B. makgabengensis</i>                       |
|-----------------------------|------------------------------------------------|------------------------------------------------|
| Height                      | To 1 m tall                                    | To 2 m tall                                    |
| Compactness                 | Dense                                          | Diffuse                                        |
| Attitude                    | Upright                                        | Upright or climbing                            |
| Leaf (attachment)           | Sessile or petioles to 1.7 mm long             | Petiolate, petioles to 8 mm long               |
| Bracteole (blade)           | Absent                                         | Present                                        |
| Bracteole length            | Up to 17.5 mm long                             | Up to 19 mm long                               |
| Bracteole colour            | Purplish turning reddish brown                 | Green turning straw brown                      |
| Calyx, outer lobes (colour) | Green or purplish turning scarious             | Green turning brown                            |
| Calyx, outer lobes (shape)  | Lanceolate or oblong-lanceolate                | Lanceolate                                     |
| Calyx, outer lobes (margin) | Subentire or with 1–3 spinulose teeth          | Entire or with 1–3 large teeth                 |
| Calyx, anterior lobe (size) | $9.7\text{--}14.5 \times 2.00\text{--}2.37$ mm | $16\text{--}18 \times 1\text{--}2$ mm          |
| Calyx, posterior lobe       | $10.2\text{--}17.5 \times 2.0\text{--}3.5$ mm  | $17\text{--}20 \times 1\text{--}2$ mm          |
| Corolla throat (colour)     | Yellow with purple stripes                     | Plain yellow or yellow with pale lilac stripes |
| Corolla, upper lobes (size) | $3.2\text{--}5.5 \times 2.4\text{--}4.0$ mm    | $6\text{--}7 \times 4.5\text{--}5.5$ mm        |



FIGURE 2.—Comparison of spininess and habitat: a, *Barleria makgabensis* in Makgabeng area; b, *B. spinosissima* in Van Collers Pass, Soutpansberg; c, natural pond close to where *B. makgabensis* was first photographed; d, *Stemodiopsis kamundii* in rocks close to pond. Photographs: a, B. Turpin; b–d, K. Balkwill.

of Custodians of Rare and Endangered Wildflowers (CREW) who joined the Magaliesberg section of the Mountain Club of South Africa on a joint exploration expedition to the Makgabeng area from 20 to 22 March 2021. The group collected 68 specimens (housed in J), representing 66 species, including the rare *Vincetoxicum coddii* (Bullock) Meve & Liede (= *Tylophora coddii* Bullock) (Turpin et al. 2536) and a new northernmost distribution record of *Chorisochora transvaalensis* (A.Meeuse) Vollesen (Turpin et al. 2535). In addition, Barbara photographed a *Barleria*, of which she did not collect a specimen, and sent it to us for identification. Two of us (WF & ID) immediately recognised the photographs as a new and as yet undescribed species allied to the spiny new species from the Soutpansberg (*B. spinosissima*) that we were working on at the time. When two of us (WF & KB) undertook fieldwork to collect *B. spinosissima* and *B. soutpansbergensis* I.Darbysh. & K.Balkwill in the Soutpansberg in early May 2021, we asked Norbert Hahn to take us to the locality in the Makgabeng area where the *Barleria* had been photographed. What ensued was a fascinating and eye-opening botanical exploration trip. Among the rocks surrounding a natural pond (Figure 2c), we collected a new locality record for *Stemodiopsis kamundii* K.Balkwill (Balkwill et al. 4244 in J) (Figure 2d) and 70 m west of the pond, we found the new *Barleria* species on a rocky sandstone ridge. There were only a few plants with very few flowers. We decided to return to the locality in May 2022 for a longer time to explore more widely. On



FIGURE 3.—Morphology of *Barleria makgabengensis*: a, climbing habit; b, thick old stem; c, old stem (hooked stem in centre) with corky bark. Photographs: K. Balkwill.

our return trip, we found many more plants of *Barleria makgabengensis* and made observations regarding its habit, e.g., climbing into trees to 2 m high (Figure 3a), and forming woody stems with corky bark (Figures 3b, c).

The Makgabeng area is located about 45 km southwest of Vivo, about 50 km west-southwest of the Soutpansberg and about 15 km south-southwest of the Blouberg (measured on Google Earth). The region is almost square in outline, orientated at about 45 degrees to an east-west line and is about 15 × 15 km in size (Figure 4). The northeastern and southeastern facing edges, as well as the eastern half of the southwestern facing edge, are escarpment-like and rise about 300 m above the surrounding plain, but the massif slopes gently down to the west. This gives Makgabeng the relief that Hahn (2011) describes

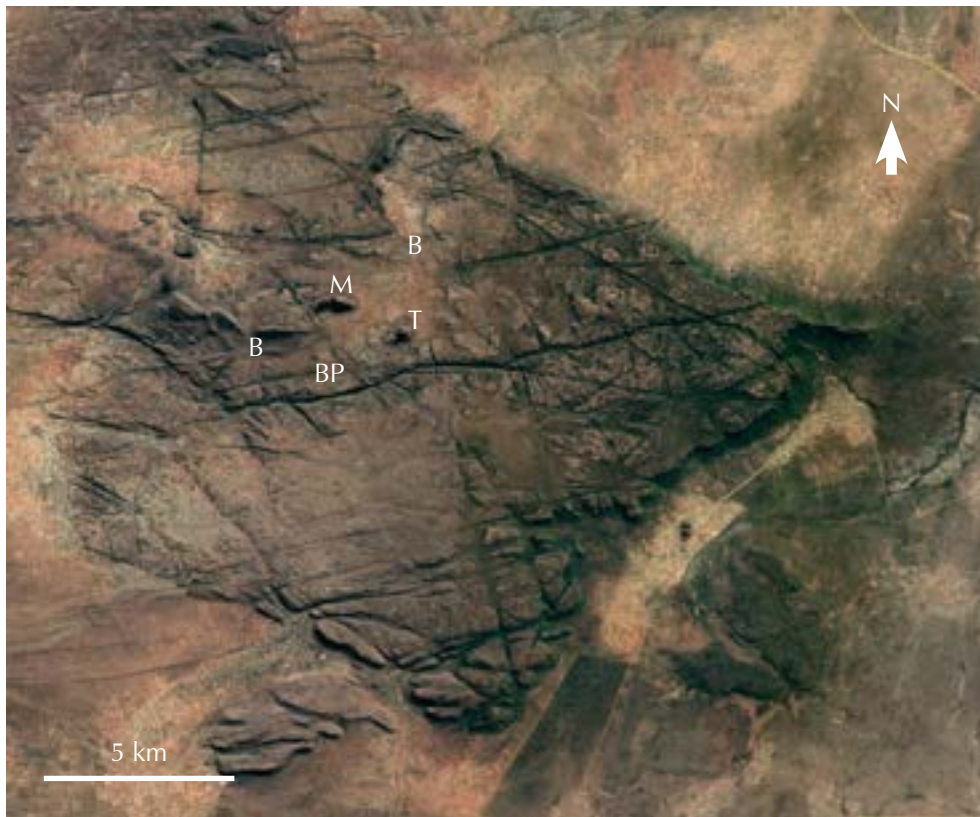


FIGURE 4.—Google Earth image of Makgabeng area: B, sites where *Barleria makgabengensis* specimens were collected; M, Masebe rock tower; P, natural pond; T, Thabanantlhana rock tower. Image: Google Earth.

as a ‘gently westerly dipping cuesta with a prominent v-shaped scarp towards the east’. The lowest point in the west has an altitude of 820 m, while the highest point, which is about 3.8 km southwest of the eastern extremity, has an altitude of 1 410 m. The area is bisected by a river that runs more or less on the diagonal from east to west, draining water from the plains on the east and eventually joining the Mogalakwena River and thence into the Limpopo River. In view of its definitive orographic features and drainage evolution, Hahn (2011) has recognised Makgabeng as a Geomorphic Province different from the Soutpansberg and Blouberg.

The rocks of Makgabeng belong to the Waterberg Group and are 1.8 billion years old (Eriksson et al. 2000). They are sandstones that display a diversity of textures, layer thicknesses and crossbedding (Simpson et al. 2002). The steep angle of some of the crossbedding suggests that it arose through dry material collapsing down the lee slope of a sand dune, rather than having been formed under water, as is usually the case (Simpson et al. 2002). This, in turn, supports the theory that the dunes were deposited by wind and that this sandstone must have been laid down under desert conditions. Fossilised mini-craters on the leeward dune faces suggest that there were high rainfall events at the time that some



FIGURE 5.—The Thabanantlhana rock tower in the northern part of the Makgabeng area stands approximately 220 m tall. Photograph: W. Froneman.

of the sediments were deposited (Simpson et al. 2002). Roll-up structures of 2–3 revolutions suggest that there must have been microbial mats that promoted cohesiveness of the surface particles implying wet periods or wet areas during the palaeoenvironment (Eriksson et al. 2000). On a map (e.g., Google Earth), it is obvious that the area is criss-crossed by many channel-like depressions. Most seem to run more or less east to west, many more or less north to south and then there are others, but usually smaller, at a range of angles. These were probably caused by faults, many of which now contain dykes (Hahn 2017). In the north of Makgabeng, there are tall towers of rock (Figure 5) formed of layered coarse material (conglomerate and sandstone) that are considered to have been laid down by rivers that ran through the palaeo-desert (Eastwood & Eastwood 2006).

The Makgabeng area is of great archaeological and historical interest. It hosts at least 600 rock art sites attributed to San hunter-gatherers (fine-line paintings of men, women and animals), Khoekhoen herders (finger paintings with circles, rays and dots) and Northern Sotho farmers (finger paintings with anthropomorphic, zoomorphic and geometric designs) (Eastwood et al. 2002). It is one of the few areas where these three rock art traditions co-occur and are sometimes overlapping, indicating potential interaction between these groups (Eastwood et al. 2002). Apron motifs occur in all three traditions and will aid in the understanding of the cross-cultural interactions (Eastwood et al. 2002).

Although the Makgabeng scarp faces occasionally receive mist, this is insufficient to develop the same mistbelt vegetation as occurs on the Blouberg and Soutpansberg. The vegetation on Makgabeng is mainly savanna growing in deep sandy soils and scrub on rocky areas (Hahn 2011). It has been classified as Soutpansberg Mountain Bushveld (SVcb21) by Mucina & Rutherford (2006). We observed the following woody species in the

savanna growing on the deep sandy soils: *Berchemia zeyheri* (Sond.) Grubov, *Boscia albitrunca* (Burch.) Gilg & Gilg-Ben., *Burkea africana* Hook., *Commiphora mollis* (Oliv.) Engl., *C. glandulosa* Schinz, *C. marlothii* Engl., *Cussonia natalensis* Sond., *C. spicata* Thunb., *Englerophytum magalismontanum* (Sond.) T.D.Penn., *Euclea crispa* (Thunb.) Gurke subsp. *crispa*, *E. natalensis* A.DC. subsp. *angustifolia* F.White, *Hexalobus monopetalus* (A.Rich.) Engl. & Diels, *Mimusops zeyheri* Sond. (an interesting small-leaved form), *Ozoroa paniculosa* (Sond.) R.Fern. & A.Fern. var. *paniculosa*, *Schotia brachypetala* Sond., *Sclerocarya birrea* (A.Rich.) Hochst. subsp. *caffra* (Sond.) Kokwaro, *Securidaca longepedunculata* Fresen. var. *longepedunculata*, *Strychnos madagascariensis* Poir.

and *S. pungens* Soler. In the sandy patches between the tree clumps, there were extensive expanses of *Xerophyta humilis* (Baker) T.Durand & Schinz and *Blepharis maderaspatensis* (L.) B.Heyne ex Roth. On rocky sheets we recorded *Barleria makgabengensis*, *Englerophytum magalismontanum*, *Myrothamnus flabellifolius* Welw. and *Vangueria parvifolia* Sond. On rocky hillsides we recorded *Aloe aculeata* Pole-Evans, *A. chabaudii* Schonland var. *chabaudii*, *A. lutescens* Groenew., *Barleria heterotricha* Lindau subsp. *heterotricha*, *Chorisochora transvaalensis* (with Balkwill & Froneman 14568 confirming the Turpin et al. 2535 collection), *Englerophytum magalismontanum*, *Entandrophragma caudatum* (Sprague) Sprague and *Ptaeroxylon obliquum* (Thunb.) Radlk. Hahn (2017) recorded five taxa that are endemic to the Soutpansberg, Blouberg and Makgabeng, namely: *Dicoma montana* Schweick., *Panicum dewinteri* J.G.Anderson, *Searsia magalismontanum* (Sond.) Moffett subsp. *coddii* (R.Fern. & A.Fern.) Moffett, *Vincetoxicum coddii* and *Zoutpansbergia caerulea* Hutch. Up to now, the only known Makgabeng endemic was *Streptocarpus makabengensis* Hilliard (Hahn 2017).

*Barleria makgabengensis* is now the second endemic species to the Makgabeng area (Figure 6) and we celebrate that in its specific epithet. The currently known subpopulations are all in the area north of the river that runs from Bodi in the east to Ga-Monyebodi in the west and bisects the plateau. It is likely that *B. makgabengensis* also occurs on the southern, less accessible, portion of the plateau. The species grows in cracks in sheets of sandstone rock (Figure 7a), or in places where there is shallow sandy soil above subterranean sheets of rock (Figure 7b). It often grows amongst woody vegetation and sometimes climbs trees and bushes to 2 m high. The current known extent of occurrence (EOO) is approximately 5.5 km<sup>2</sup>, but the occurrence is likely to be much wider. Although the habitat requirements are relatively specific, much of the area fulfils the requirements. A few plants showed signs of browsing, but these represented a very small proportion of all the plants seen. The area is recognised as a heritage site and thus is afforded a certain level of protection (Namono 2018). We thus recommend a provisional Red List threat status of Least Concern.

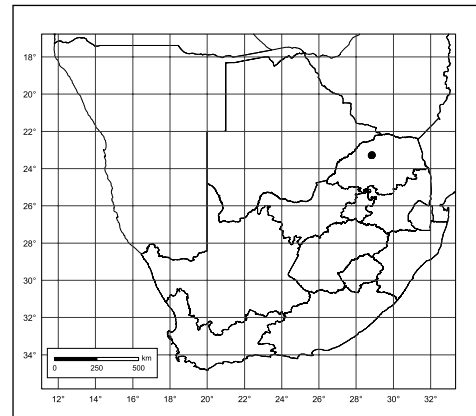


FIGURE 6.—Known distribution of *Barleria makgabengensis* in southern Africa, based on herbarium specimens listed in the text.



FIGURE 7.—Habitat of *Barleria makgabengensis*: a, in cracks in rock sheet (light green plants); b, in sand on top of rock sheets. Photographs: K. Balkwill.

Plants have been photographed or collected in flower from March to May and, on the basis of how many young buds were still developing on plants by mid-May 2022, the flowering time probably extends into June. Capsules were found on plants in May and the fruiting period possibly extends into July.

#### Additional specimens examined

SOUTH AFRICA, Limpopo: **2328** (Baltimore): about 1 km southwest of Masebe, 1057 m (–BD), 18 May 2022, *Froneman & Balkwill* 1314 (GLOW, K, PRE); about 1.9 km south of Masebe, 1119 m (–BD), 5 May 2021, *Balkwill et al.* 14243 (E, J, MO); about 2.3 km northeast of Masebe, 1087 m (–BD), 18 May 2022, *Balkwill & Froneman* 14576 (J, K).

**Description.**—Spiny erect suffrutex 0.3–1.0 m tall or a scrambler to 2 m when growing between shrubs and trees. *Stems* arising from a woody rootstock and branching above the ground, young stems green, densely covered with numerous white, patent, bristly hairs and stalked glands to 0.5 mm long; older stems glabrescent, oldest stems with corky bark. *Axillary spines* derived from bracteoles of aborted (sterile) inflorescences, stalked, paired, stalk 3–7 mm long, spines 4–12 mm long, straw-coloured. *Leaves* broadly ovate or elliptic to almost round, 9–26 × 7–18 mm, base cuneate and attenuate, apex acute with a conspicuous mucro about 2 mm long; adaxial surface with 1 mm long ascending eglandular hairs scattered throughout, margins and veins with additional fine hairs to 0.3 mm long, margins near tips also bear multicellular hump-shaped structures that sometimes bear a hair; abaxial surface with both 1 mm long ascending eglandular hairs and fine hairs to 0.3 mm long restricted to veins; secondary veins 3–5 per side; petiole 2–8 mm long. *Inflorescence* axillary in the upper branches; cymes unilateral 2–4(6)-flowered and often with an additional sterile node, 25–40 mm long, lax, simple; peduncle 4–8 mm long; internodes of rachis 5–8 mm long; indumentum of peduncle and rachis of dense patent eglandular and stalked glandular hairs about 0.3 mm long. *Bracts* leaflike. *Bracteoles* lanceolate, spinose, unequal in length; blade present, about 0.3 mm wide on each side of midrib, 5–19 × 1–2 mm, mid-vein thick, with white ascending eglandular and patent gland-tipped hairs about 0.3 mm long, margins entire. *Calyx* outer lobes lanceolate, covered with white ascending eglandular and gland-tipped hairs about 0.5 mm long and many eglandular hairs about 0.25 mm long on the external side, denser at base, blade green turning brown becoming scarious, midvein

prominent, with 4–5 secondary veins from base on each side of midrib, margins entire or sometimes with 1–3 spines on the upper half; anticous lobe  $16\text{--}18 \times 1\text{--}2$  mm, apex usually single-spined, sometimes 2-spined; posticous lobe  $17\text{--}20 \times 1\text{--}2$  mm; inner calyx lobes sub-similar to posticous lobes, but shorter. *Corolla* with fine wispy hairs externally, glabrous within except where filaments are attached; lobes blue or mauve, lower lobes elliptic to obovate,  $9\text{--}13 \times 7\text{--}9$  mm, upper lobes  $6\text{--}7 \times 4.5\text{--}5.5$  mm; throat yellow and sometimes with faint lilac lines; tube yellowish light green, 18–19 mm long, 3 mm wide for bottom 7 mm, then constricted to 2 mm wide for 3 mm, then flaring out to 5–6 mm wide at apex. *Stamens* 2, 21–23 mm long, exerted by about 13 mm, inserted 9 mm above the base of the corolla tube; filaments white, adnate for 3 mm and free for 20–22 mm, with retrorse eglandular hairs from about 1 mm above point of insertion downwards along the adnate portion; anthers purple, 3–4 mm long, lateral staminodes with filaments adnate for 3 mm, then 3 mm long, with retrorse eglandular hairs from about 1 mm above point of insertion downwards along the adnate portion, antherodes 0.6–1.0 mm long, adaxial staminode with filament adnate for 3 mm, then 2 mm long, with retrorse eglandular hairs from about 1 mm above point of insertion downwards along the adnate portion, without antherode. *Disc* cylindrical, sleeving ovary, 1.5 mm high, 2 mm in diameter, distal edge scalloped. *Gynoecium* with ovary ovoid,  $3 \times 1.6$  mm, glabrous except for a few stiffish hairs near apex; style 30 mm long, exerted for about 15 mm, glabrous; stigma cylindrical,  $1 \times 0.7$  mm, slightly wider than style, surface papillate. *Capsule* dark shiny brown, oblong, fusiform  $13\text{--}16 \times \pm 6 \times \pm 3$  mm, with a few stiff eglandular hairs towards the apex; retinacula 3 mm long, light brown. *Seeds* discoid, about 4.5 mm in diameter, with dense hygroscopic hairs, shiny silvery brown. *Flowering time*: March–June. Plate 2399.

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PLATE 2400 *Oldenburgia grandis*

*Oldenburgia grandis*

Asteraceae

South Africa

**Oldenburgia grandis** (Thunb.) Baill. in *Histoire des Plantes* (Baillon) 8: 97 (1882). *Arnica grandis* Thunb. 2: 154 (1800). *Oldenburgia arbuscula* DC. 7(1): 12 (1838).

On seeing the hunched form of *Oldenburgia grandis* along a mountain slope (Figure 1a), one could be forgiven for disbelieving its placement within the Asteraceae. Its robust, gnarled trunk and stiff, spreading branches covered in dark, thick and corky bark seem out of place within the daisy family. These long-lived trees can reach 5–6 m in height with a crown composed of large, stiff and leathery leaves and each leaf up to 360 × 150 mm, oblong, oblanceolate or obovate, with the leaf margins rolled inwards and the surface rounded above. Young leaves are silvery white and densely covered with matted, woolly hairs, while mature leaves are deep green and shiny with velvety white undersides and broad, protruding midribs. On closer inspection of the flower heads, however, the species' familial ties become clearer. Each flower head resembles a giant thistle with its short, wide, purple brush covered thickly with white hairs (Figure 1b). These are borne on long, stout, velvety white peduncles that emerge above the crown from the centre of a rosette of leaves.

The pioneering Victorian artist, Marianne North, visited Grahamstown (now Makhanda) in December 1882 and painted a vibrant portrait titled 'A Mountaineer from the Hills near Grahamstown' (JSTOR 2023) commenting that she thought it was 'a most striking shrub' (North 1893). The distinctive appearance of *Oldenburgia grandis* has long intrigued residents of the Makhanda area, with its form used in the logo of the Makhanda branch of the Wildlife Society of South Africa (WESSA) (Figure 2a), as well as the Department of Botany at Rhodes University (Figure 2b). It is also the namesake of the Oldenburgia Hiking Trail, which meanders through the slopes on which it grows, the Oldenburgia Hiking Club (Figure 2c), and the annual Oldenburgia Marathon. Even a beer, Oldenburgia White Beer, produced by Featherstone Brewery, is named after this local iconic species (Figure 2d).

The various common names for *Oldenburgia grandis* are typically reference to its characteristic features and include the likes of rabbit's ears, lamb's ears and donkey's ears, all of which conjure up the shape and soft, woolly texture of the ears of young rabbits, lambs or donkeys. Both the Afrikaans name, *bastersuikerbos*, and the Xhosa name, *isiqwane*, indicate the likeness of *O. grandis* to large proteas, especially when seen from a distance – and it is one of the few non-Proteaceae taxa covered by the Protea Atlas Project (2023) as a so-called honorary protea. Other common names, such as mountain hunchback and the Afrikaans *kreupelboom*, emphasizes the plant's gnarled and twisted growth form and thick, corky bark.

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PLATE 2400.—1, branch with densely tomentose young leaves, × 1; 2, developing capitulum, × 1. Voucher specimen: living collection 984/13 – 737, Kirstenbosch National Botanical Garden, Cape Town. Artist: Gillian Condy.



FIGURE 1.—*Oldenburgia grandis* in habitat: a, short tree with thick, gnarled trunk and branches covered in thick corky bark; b, florets are densely packed in large terminal capitula with a fringe of spindly white or pink ray florets surrounding the mass of white disc florets; c, inflorescences are visited primarily by specialist flower-visiting birds including Malachite Sunbirds (shown) and Cape Sugarbirds; d, fertile cypselae have stiff pappus bristles, which likely provide some degree of wind dispersal for the seeds; e, plants are largely restricted to rocky fire refugia and can tolerate low intensity fires. Photographs: C.I. Peter.

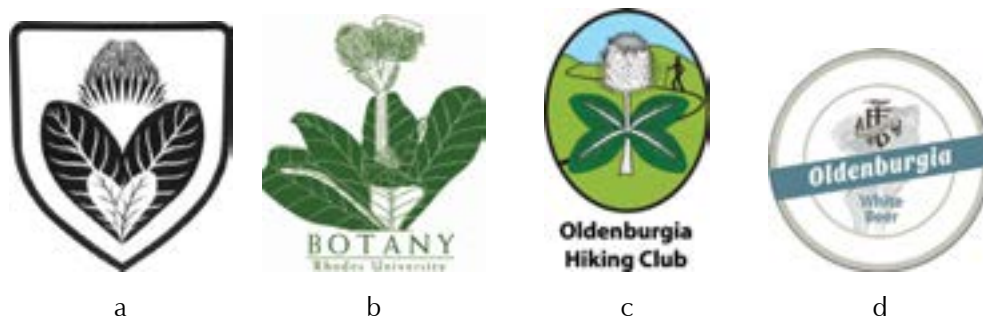


FIGURE 2.—*Oldenburgia grandis* features in multiple logos: a, the Makhanda branch of WESSA; b, the Department of Botany at Rhodes University (artist: Carin Swart); c, the Oldenburgia Hiking Club; d, as the namesake and on the label of Featherstone Brewery's Oldenburgia White Beer.

*Oldenburgia grandis* is one of four species in the genus, which is endemic to the Western and Eastern Cape of South Africa. The generic name honours Franz Pehr Oldenburg, a Swedish soldier for the Dutch East India Company, who accompanied the botanists Thunberg and Masson on some of their travels in the Cape in the early 1770s. The four species of the genus *Oldenburgia* form the monotypic tribe Oldenburgieae (Ortiz 2009; Ortiz et al. 2013). Originally included in the Mutisieae (Bond 1987), a basal tribe of the Asteraceae better represented in South America (Goldblatt 1987), the genus *Oldenburgia* was considered to have stronger links to South American than African genera of Mutisieae (Bond 1987). *Oldenburgia grandis* also bears a remarkable resemblance to *Raiguenrayuncura* Barreda, Katinas, Passalia & Palazzesi, a fossil Asteraceae from Argentina from approximately 47.5 million years ago (Barreda et al. 2012). The intriguing possibility of an ancient biogeographic link with South America was, however, refuted by more recent molecular phylogenetic studies. These have placed the monotypic Oldenburgieae, together with tribe Tarchonantheae (which includes the genera *Tarchonanthus* and *Brachylaena*) in the subfamily Tarchonanthoideae (Susanna et al. 2020). All members of this subfamily are woody and are indigenous to mainland Africa or Madagascar.

*Oldenburgia grandis* is endemic to grassy fynbos, or more rarely, mountain fynbos in the Eastern Cape Province of South Africa (Figure 3). The species occurs between the Zuurberg and the Kap River estuary – a range of some 200 km – and is always associated with outcrops of Witteberg Quartzite where it grows on nutrient-poor sandstone and quartzitic soils.

The habitat of *Oldenburgia grandis* is prone to frequent, low intensity, grass-fuelled fires. Apparent adaptations to these fires include thick, insulating bark and the capacity to resprout from the rootstock. Intense fires can kill individuals of *O. grandis*, however, and populations are typically found on rocky outcrops, which provide some refuge from hotter fires (Swart 2008; Figure 1e). This is particularly important for seedlings and saplings that do not have the ability to resprout after fire, as was observed at Dassie Krantz near Makhanda, where a seedling growing on rock was completely undamaged, while the surrounding vegetation was charred after a fire. A detailed study of the population dynamics of *O. grandis* (Swart 2008) found that most populations were stable, but that severe fires could destroy large numbers

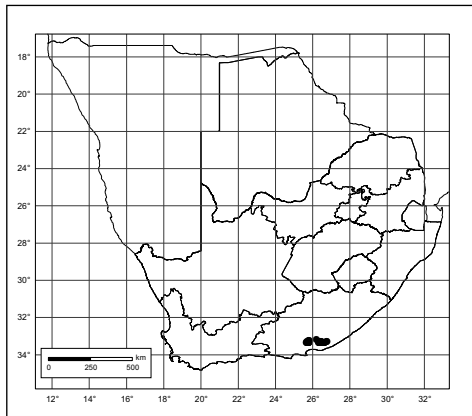


FIGURE 3.—Distribution of *Oldenburgia grandis* in the Eastern Cape Province, South Africa.

of individuals. Therefore, dense stands of non-indigenous woody plants that greatly increase fuel loads pose a threat to *O. grandis*, as they cause more intense fires.

*Oldenburgia grandis* flowers from October to January (Bond 1987), but unopened capitula can be seen year-round. Flower production in individual plants varies strongly between years. Prior to 2022, little was known about the pollination biology of *O. grandis*. Vogel (2015) predicted that the species was rodent pollinated, based on Bond's (1987) emphasis on the similarity of *O. grandis* to *Protea* species pollinated by rodents, as well as the low placement of capitula in other species of *Oldenburgia*.

In contrast to Vogel's prediction, the only pollinator observations reported were by a Cape Sugarbird to plants cultivated at Kirstenbosch National Botanical Garden, which fall outside of the species' natural distribution range (Rebello 1987).

Using camera traps, field observations and pollinator exclusion experiments, Mostert (2022) determined that *Oldenburgia grandis* is pollinated by specialist nectivorous birds. The stiff leaves and large, robust brush inflorescences serve as perches. Large quantities of diluted nectar are produced, which leaks out of individual florets and seeps into the tightly packed space between inflorescences where it is accessible to birds. Malachite Sunbirds (Figure 1c) were the most frequent visitors, but Cape Sugarbirds appeared to be the more effective pollinators, as they were more likely to perch with their feet on top of the capitulum, more commonly fed from the centre of the capitulum, and were more frequently observed with pollen on their feathers than sunbirds.

Mostert (2022) found no evidence of fire stimulated seed release or germination and overall it appears that recruitment from seed is sporadic but not linked to fire events. Reproduction from seed appears to be rare, although fertile seeds (Figure 1d) are easily germinated. Low natural recruitment may partially be explained by high rates of seed predation by the larvae of a Tephritid fly, a common daisy seed predator. The life history strategy of *Oldenburgia grandis* is typical of a long-lived species that tends to allocate resources to persistence and resistance to disturbances, rather than to growth or fecundity. Persistence of the populations thus relies strongly on adult survival (Swart 2008).

**Description** (after Bond 1987 and Bredenkamp 2019).—Shrub or small tree, 1–6 m tall with gnarled, rough, dark stems and branches covered in thick corky bark. Leaves oblong, oblanceolate or obovate with obtuse or subacute apices, up to 360 × 150 mm; densely tomentose when young, with the dense, white, woolly hairs persisting abaxially and becoming glabrous adaxially at maturity. Peduncles to 500 mm long, densely tomentose, bearing several

leaf-like bracts and 3–5 cymosely arranged capitula. *Involucre* cyathiform, up to 80 × 80 mm; involucre bracts numerous, about 10-seriate, narrowly lanceolate and closely imbricate, but with reflexed acuminate tips, 15–40 mm long, ± 3 mm wide at base, dark maroon with white-tomentose bases. *Ray florets* ± 60, sub-uniseriate, white or pale pink; tube ± 15 mm long; outer lip 3-toothed, 16–22 × 2 mm; inner lobes 11–15 × 0.5–1.0 mm; anthers ± 14 mm long, including tails of 4 mm long; style up to 35 mm long; cypselae fusiform, glabrous, 10-ribbed, 12–15 × 1.5–3.0 mm; pappus of about 18 barbellate bristles of uniform length and thickness, ± 25 mm long. *Disc florets* ± 800, white; tube 14–16 mm long; lobes 14–16 mm long; anthers 10–17 mm long, including tails of 3–5 mm long; style 30–37 mm long. *Fruit* cypselae 12–15 mm long, 20–26 pappus bristles, each 30 mm long. Plate 2400.

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## Guide for authors and artists

### INTRODUCTION

Contributions from authors and artists are most welcome. The policy of the editorial committee of *Flowering Plants of Africa* (FPA) is to obtain contributions from as wide a range of authors and artists as possible and to depict a rich and interesting mix of plants from all over Africa. SANBI reserves the right to purchase original artwork and retain copyright for FPA. All contributions are assessed by referees.

Plates that have already been published in colour in another journal or magazine are generally not acceptable for FPA.

Authors and/or artists are advised to contact the editor (Alicia Pretorius) before any work is undertaken with a view to publication in FPA: a.grobler@sanbi.org.za.

### AUTHORS

All plates published in volumes 1–49, are listed in the *Index* published in 1988. There are, however, several completed plates awaiting publication in FPA. Authors intending to have plants illustrated and written up for FPA are therefore advised to contact the editor to establish whether a plant has not already been figured for FPA.

Authors are expected to supervise the execution of plates to ensure that they are botanically correct. As detailed under the section 'Artists', a write-up and/or plate will not be acceptable unless a voucher specimen is made of the figured specimen and preserved in a recognised herbarium.

Before writing up a contribution for FPA, the author should ascertain whether the plate has been approved by the journal's panel of referees consisting of both botanists and botanical artists. Only after approval of the plate, should the author produce the text for submission to the editor. Approved contributions will be published when space allows. Those in which the names of new taxa are published for the first time usually receive priority.

Manuscripts should be submitted electronically to the editor by June 2024 and should conform to the general style of the most recent issue of FPA. From volume 58 onwards, literature references are treated as described under headings 1, 2 and 3 further on.

The following serves as a checklist of requirements for an FPA contribution:

1. **Synopsis.** The correct name of the plant together with its author/s and relevant literature is cited. Put a comma after the author's name if the publication that follows is his/her own; write the word 'in' after the author's name if the publication that follows is a

journal or other work edited/compiled by someone else. Following this, are synonyms (listed chronologically) plus their author/s and relevant literature reference/s reflecting only author, page and year of publication, e.g., Boris et al.: 14 (1966). The whole synopsis is in one paragraph. If there are many synonyms and literature references, restrict yourself to the most important ones. References should be arranged in chronological sequence; where two or more references by the same author are listed in succession, the author's name is repeated with every reference. Author citations of plant names should follow Brummitt & Powell (1992, *Authors of plant names*); for other authors, give full surnames followed by a colon, page number/s and date.

2. **Literature references in the text.** Should be cited as follows: 'Jones & Smith (1999) stated ...' or '... (Jones & Smith 1999)' when giving a reference simply as authority for a statement. When more than two authors are involved, use the name of the first author followed by 'et al.' Two or more references should be listed chronologically, e.g., '(Smith 1996, 1998, 2013; Nel 2001; Bester et al. 2007)'. Personal communications are given only in the text, not in the list of references; please include full initials to identify the person more positively. Referencing websites are generally discouraged unless their content is based on reviewed scientific research (e.g., databases of plant names, online Floras, specimen images, Red Lists, etc.) or are otherwise trustworthy and reputable.
3. **List of references.** All publications referred to in the synopsis and the text, but no others, are listed at the end of the manuscript under the heading 'References'. The references are arranged alphabetically according to authors and chronologically under each author, with a, b, c, etc. added to the year if the author has published more than one work in a year. If an author has published both on their own and as senior author with others, the solo publications are listed first and after that, in strict alphabetical sequence, those published with one or more other authors. Author names are typed in capitals. Titles of books and journals are written out in full, in italics. In the case of books, the name of the publisher is followed by a comma and the place of publication. For websites, provide full website name, address and the date when it was accessed in brackets.
4. **Text proper.** It should be written in language and style acceptable to both the scientist and informed lay person. The following features should, as far as possible, be described and discussed in the text:
  - Main diagnostic characters for a brief pen picture of the plant.
  - Affinities: how the taxon differs from its nearest allies; if necessary, keys or tables may be used to distinguish closely related taxa.
  - History of the taxon, where and when first collected and by whom.
  - Geographical distribution in Africa: a distribution map, which will be handled as a figure, is essential; authors should submit a list of quarter degree grid cells, or GPS coordinates in decimal degrees in two columns (first column for latitude, second column for its corresponding longitude), from which the editor's office will produce the distribution map.
  - Ecology: habitat preferences etc. It is highly recommended that authors submit a photograph of the plant in habitat or a general habitat image.

- Phenology: time of flowering, fruiting, etc.
  - Economic importance, edibility, medicinal use, toxicity, etc.
  - Cultivation potential and hints on cultivation.
  - Origin of the scientific names.
  - Common names in various languages.
  - Any other facts of interest to the scientist or lay person.
5. **Description.** This is a formal description of the taxon and not merely of the specimen illustrated. For measurements, use only units of the International System of Units (SI). Use only mm and/or m.
6. **Photographs and captions.** Supply a caption for the colour plate, indicating the relevant magnifications and/or reductions, and citing the voucher specimen used for the illustration, i.e., collector + number + herbarium where the specimen is housed. The plate's caption ends with the name of the artist. Also supply captions for the distribution map and any other figures (please use scale bars where relevant), making sure that all figures are mentioned in the text. All photographs should be submitted as unedited high-resolution files. Composites will be created by the graphic designer from original photographs; amend captions for these appropriately, with a, b, c, etc.

## ARTISTS

1. **Supervision.** All illustrations should be executed under the supervision of the botanist writing the text to ensure botanical accuracy and that details considered important by the botanist are adequately depicted.
2. **Dimensions.** The dimensions to work to are 160 × 210 mm (width × height of image) or slightly smaller. Illustrations are printed as is, i.e., the same size. Only in exceptional cases are illustrations reduced or enlarged.
3. **Paper.** The paper must be of good quality and as white as possible. Arches or Saunders Waterford (hot-press, 300 gsm) is recommended. The use of board should be avoided.
4. **Watercolours.** The use of good-quality watercolours, e.g., Winsor & Newton (certain pigments fade with time) or Schmincke (colourfast), is essential. The use of black paint is not recommended as it is too harsh and tends to kill colour. Similarly, white paint must be used with caution since it tends to dull adjoining colours and sometimes reproduces as a bluish colour. Its use should be limited to white hairs and certain highlights only. To reflect whiteness, endeavour to use the paper colour itself.
5. **Subject material, composition etc.** For obvious reasons, the subject material should be representative of the species being illustrated and should be in excellent condition. Drawing from photographs is not recommended: it is impossible to obtain the same detail from a photograph as from the living plant.

All parts should be measured by the artist and magnifications indicated on the back of the plate and the figure(s) where relevant.

The plate should not be overcrowded with too many small dissections. These should preferably be inserted as separate figures in the text. Dissections or habit sketches included on the plate should be in pencil or colour, not ink, whereas dissections or habit sketches to be used as separate text figures should be in ink.

A voucher specimen made of material from the plant(s) illustrated, must be preserved, given a collector's number and housed in a recognised herbarium as a permanent record. This is most important: without a cited voucher specimen, the plate and write-up will not be accepted.

Show clearly as many features as possible, for example apical buds, leaf axils, hairs, glands, bracts, stipules, upper and lower surfaces of leaves showing venation, front, side and back view of flowers, mature fruit, habit and where necessary and feasible, the underground parts. The supervising botanist will know which features require accentuation.

The artist's signature must be unobtrusive but clearly written so that it will stand reproduction. Numbering of plant parts should be done in light pencil: permanent numbering will be in consultation with the editor. No other annotations should appear on the plate. Information such as species name, collector's name and number, date, locality, magnifications etc. should be written on the back of the plate.

- 6. *Dispatch of plates.*** Plates should be carefully packed, flat, using a sheet of Masonite or similar material to prevent bending, and sent by courier or insured post.



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## Other publications of the South African National Biodiversity Institute

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# Flowering Plants of Africa

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