Flowering Plants of Africa

Volume 67 June 2021

Celebrating 100 years: 1921–2021

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 are mostly prepared by artists on the staff of the South African National Biodiversity Institute (SANBI), but we welcome other contributions of suitable artistic and scientific merit. Please see *Guide for authors and artists* on page 214.

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(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

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Cover illustration: *Adenia repanda* (Plate 2373)

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Flowering Plants of Africa

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Edited by

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with assistance of

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This volume is dedicated to

GIDEON FRANCOIS SMITH, Ph.D. (20 October 1959–)

Prof. Gideon Smith in the H.G.W.J. Schweickerdt Herbarium, Department of Plant and Soil Sciences, University of Pretoria, where he held the John Acocks Chair in Botany. Photograph: K. Oberlander.

As plant scientist and institutional manager, Prof. Gideon Smith has held tenured and temporary positions as Chief Director for Research, Chief Director for Biosystematics, Chief Financial Officer, and Chief Executive Officer at the South African National Biodiversity Institute. He simultaneously held the John Acocks Chair in Botany at the University of Pretoria, and is at present attached to the Nelson Mandela University in Gqeberha [Port Elizabeth]. During a career of 40 years Gideon made significant and enduring contributions to botanical science, especially plant systematics, in southern Africa and beyond. He is a past President of the International Organization for Succulent Plant Study (IOS) and has held various positions on the councils and steering committees of national and international botanical initiatives, including the Species Plantarum-World Flora Project, Global Plants Initiative, International Association for Plant Taxonomy, World Flora Online project, Southern African Botanical Diversity Network, the South African Biodiversity Information Facility, and the South African Association of Botanists.

Gideon is South Africa's most prolific author on Old and New World succulents and has authored or co-authored over 1 000 scientific and other papers, as well as more than 50 books. Cacti and succulents have been a primary research focus, most especially the aloes and their kin (family Asphodelaceae) and the *plakkies* (family Crassulaceae). Gideon collaborates freely and easily, and has inspired and worked with scores of emerging and established colleagues from around the world. In recognition of his inspired leadership, mentoring, training of students, wide-ranging research outputs, and community service he has received more than 15 medals and other awards, including the prestigious *Cactus d'Or* instituted by the late Princess Grace of Monaco, with the cooperation of the Principality and the IOS.

As an avid supporter of botanical art, he has contributed almost 50 species monographs, especially of African and Madagascan succulents, that have accompanied plates published in *Flowering Plants of Africa* (*FPA*). He is commemorated in the species name *Crassula smithii* that was treated and illustrated as Plate 2286 in volume 63 of *FPA*. It is fitting that this 67th volume of *FPA* be dedicated to Gideon, whose informative contributions on regional kalanchoes greatly enhance its pages.

PLATE 2361 *Xerophyta adendorffii*

Xerophyta adendorffii Velloziaceae

South Africa

Xerophyta adendorffii *Behnke* in Behnke et al., Botanical Journal of the Linnean Society 172: 50 (2013).

The Velloziaceae is an ancient monocot family with its centre of diversity in South and Central America. Elsewhere the family is represented mainly in Africa and Madagascar, with one species of *Xerophyta* in southern Arabia and a monotypic genus, *Acanthochlamys*, in southwestern China (Behnke et al. 2013; Mabberley 2017). Crown ages of ~115 Ma (Mello-Silva et al. 2011), or (97–)74.3(–52) Ma (Alcantara et al. 2018), have been proposed for the family. Molecular and morphological evidence supports a Gondwanan origin for Velloziaceae, with a vicariant pattern of distribution. The clade representing the genera *Xerophyta* and *Talbotia* is confined to Africa, Arabia and Madagascar, and is uniquely supported by capsules with basal loculicidal dehiscence (Mello-Silva et al. 2011).

The monotypic genus *Talbotia*, based on the South African *T. elegans*, is morphologically distinct and has long been recognised as a separate genus (e.g. Coetzee et al. 1973; Smith & Ayensu 1974; Dyer 1976; Kubitzki 1998; Leistner 2000). However, following combined molecular and morphological studies, *Talbotia* was transferred to *Xerophyta* by, amongst others, Mello-Silva et al. (2011). This lumper's approach was also followed in the most recent revision of African Velloziaceae (Behnke et al. 2013), resulting in *Xerophyta* currently being accepted by botanists of the phylogenetic school as the only genus representing the family on the African continent. Behnke et al. (2013) recognises 45 species of *Xerophyta* in Africa, including the recently described *X. adendorffii*, subject of the present contribution (Figures 1–4). Based on growth form and macromorphology, most members of *Xerophyta* in southern Africa can be divided into two distinct groups, for convenience here referred to as a Shrub Group and a Herb Group.

The Shrub Group in *Xerophyta* have sturdy, relatively thick erect stems, 0.2–5.0 m long, often with 'woody' branches, all covered with a dense layer of closely packed persistent leaf sheaths, the leaf blades being deciduous. Species in this group are particularly fire resistant due to protection provided by the mantle of non-flammable (probably mainly due to the exclusion of oxygen) dead leaf bases. Plants in this group are commonly referred to, amongst others, as black-stick lilies or *bobbejaansterte* (Afrikaans), both names referring to the persistent black fire-charred stems, which are a conspicuous feature in recently burned grassland or savanna. One species of this group, namely *X. retinervis* (= *Vellozia retinervis*), has previously been figured in this series (Dyer 1942, plate 856).

The Herb Group in *Xerophyta* are low-growing, usually mat-forming perennial herbs with the stems relatively slender and less than 200 mm long when erect, or up to 400 mm

PLATE 2361.—Flowering tuft of plants, in natural habitat on chert-impregnated dolomite rocks, × 0.1. Voucher specimen: *Hyde-Johnson 105* in H.G.W.J. Schweickerdt Herbarium, Pretoria. Artist: Jenny Hyde-Johnson.

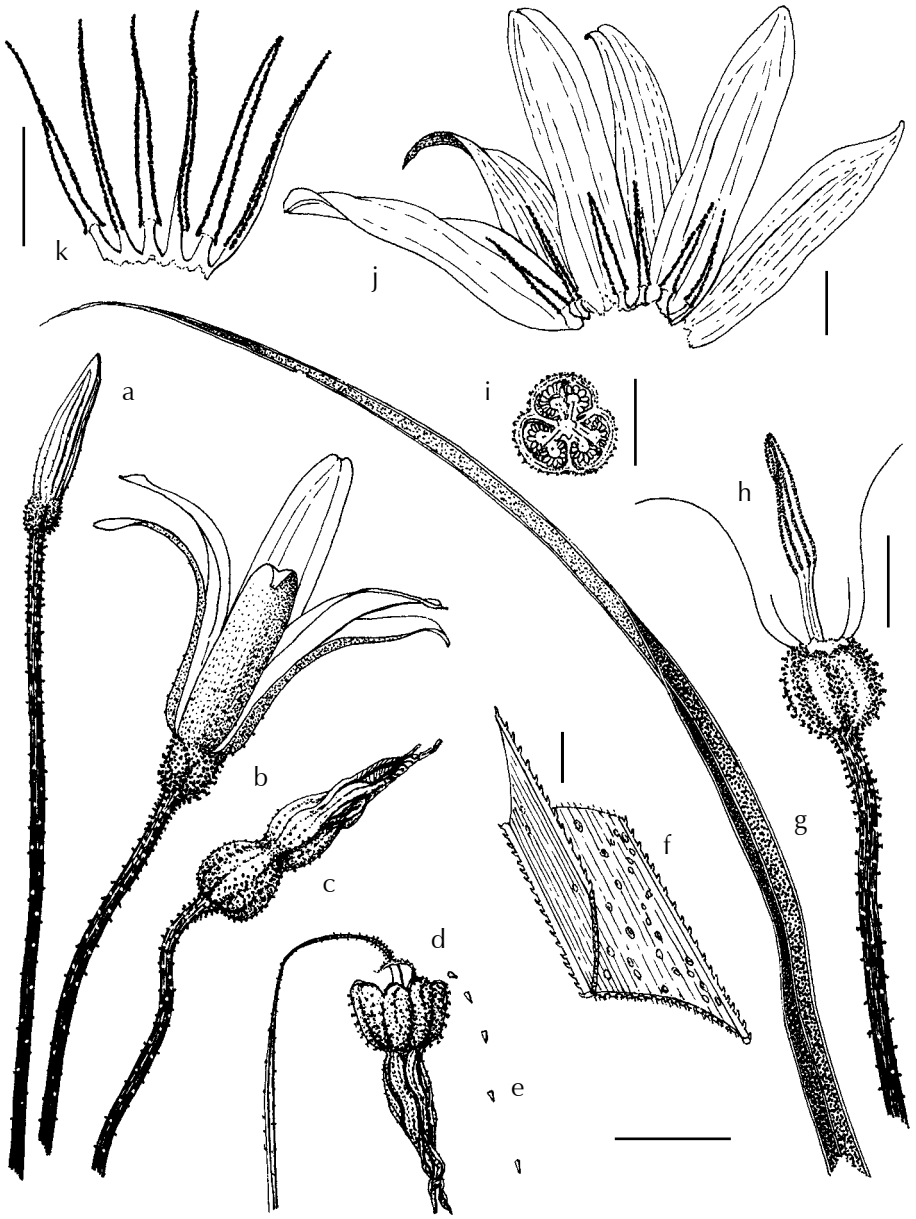

FIGURE 1.—*Xerophyta adendorffii*, details of leaf, flower and fruit morphology: a, flower bud; b, open flower; c, faded flower with developing fruit; d, ripe capsule with dry, persistent perianth dehisced with three slits at the base; e, seeds being released upon shaking of capsule by the wind; f, section of mid-blade showing serrulate margins and keel, the serrations pointing towards the leaf apex; g, relatively young rehydrated leaf, but with distal part remaining conduplicate; h, partly stylised flower showing style with elongated stigma, and gland-covered inferior ovary and pedicel; i, transverse section of ovary with axile placentation on intrusive placentas; j, perianth opened out to show insertion of stamens at base of tepals; k, androecium opened out to show difference in size of anthers between inner (broader) and outer (narrower) series. Horizontal scale bar: a–e, g, 10 mm. Vertical scale bars: f, 1 mm; h–k, 5 mm. Artist: Jenny Hyde-Johnson.

long when decumbent, and with the leaf blades deciduous or persistent. Although plants are fire-adapted, they tend to favour more protected sites such as shallow soils on rocky outcrops, in particular around the edges of sheets of exposed rock. Because of the often xeric conditions of this type of habitat, at least some of the species in this group are resurrection plants. *X. longicaulis*, the second species of *Xerophyta* to have been figured in this series, belongs to this group (Crouch & Condy 2009, plate 2246). The latter species, as well as *X. elegans* (= *Talbotia elegans*), are, however, exceptions in that both prefer moist rather than xeric habitats (Crouch & Condy 2009).

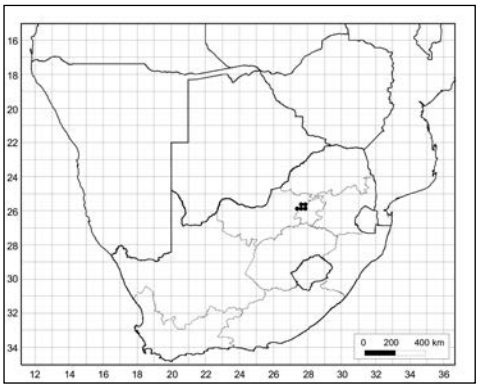

FIGURE 2.—Known distribution of *Xerophyta adendorffii*.

Xerophyta adendorffii, a member of the Herb Group, is a restricted-range, but locally common, species confined to the outcrops of dolomite with chert inclusions to the northwest of Pretoria, South Africa (Skurweberg and Witwatersberg, including parts of the Cradle of Humankind, a World Heritage site) and quartzitic outcrops on parts of the nearby Magaliesberg (Figure 2). Its distribution range straddles the border between Gauteng and North West provinces. The only other species of the Dwarf Group in Gauteng and North West is the widespread *X. humilis* and *X. schlechteri*. *Xerophyta adendorffii* and *X. schlechteri*, both with predominantly white, funnel-shaped flowers, are closely related and previously both were treated as part of a broadly defined *X. viscosa* (e.g. Coetzee et al. 1973; Coetzee 1974). An analysis of *rbcL* sequence data indicated that *X. adendorffii* is sister to a clade comprising *X. schlechteri* as well as *X. rosea* and *X. rehmannii*, the latter two species occurring in Limpopo and Mpumalanga provinces. These four species, in turn, are sister to *X. seinei*, a restricted-range species from Zimbabwe (Behnke et al. 2013). *Xerophyta humilis*, on the other hand, is a very distinct species with nearest relatives in Madagascar rather than Africa (Behnke et al. 2013). It is easily recognised by its plate-like, usually mauve to purple flowers, with the outer tepals conspicuously aristate.

The specific epithet of our species honours Jacobus [Jaco] Daniël Adendorff (1972–), a chemical engineer by training. Already during his school years in Pietermaritzburg, Jaco enjoyed exploring the KwaZulu-Natal Midlands and the Drakensberg for wild flowers, and in the process came to know many species, including *Xerophyta viscosa*. On completion of his tertiary studies at the University of Pretoria, Jaco was employed by the Nuclear Energy Corporation of South Africa (NECSA), the premises of which is near Pelindaba and within the distribution range of *X. adendorffii*. In his free time, he examined the rich flora of the surrounding areas and combined his interest in plants with his other hobby, photography. Jaco is particularly skilled in the specialised fields of ultraviolet (UV) and infrared (IR) photography; the former plays an important role in pollination biology (Adendorff 2008). To identify plants in the area, he used amongst others, the *Field guide to the wild flowers of the Highveld* (Van Wyk & Malan 1988). In this publication is depicted a white-flowered species of *Xerophyta* under the name *X. viscosa* (p. 91, t. 177). Being familiar with the concept

of *X. viscosa* in KwaZulu-Natal, Jaco was intrigued by the fact that these very different-looking plants in the dolomitic hills around NECSA carried the same name. He tried to find a local botanist with an interest in the taxonomy of *Xerophyta*, but was referred to Prof. H.-Dietmar Behnke of the Ruprecht Karl University of Heidelberg, Germany, who at the time was working on a revision of the genus. Following some exchanges of letters and plant material between the two, Jaco's interest in the taxonomy of *Xerophyta* was stimulated and a very fruitful collaboration developed between him and Prof. Behnke. Over a period of

FIGURE 3.—*Xerophyta adendorffii*, a resurrection plant, at Kalkheuvel West, Broederstroom, South Africa: a, bright green, fully rehydrated plants in summer growing as dense mats in shallow soil on an outcrop of dolomite in grassland (visible in background); b, desiccated leaves about three days after an unseasonal heavy rain shower during winter assumed a mostly dark reddish maroon colour before turning green after about seven days; c, desiccated leaves showing typical yellow colouration upon rehydration, eventually turning green over a period of two to three days; a similar yellow colour is displayed by leaves undergoing desiccation. Photographs: A.E. van Wyk.

about four years, Jaco did extensive fieldwork on several members of *Xerophyta* in South Africa and provided Prof. Behnke with valuable observations and plant material. Today the species whose identity he initially questioned, very aptly and deservedly carries his name. In 2019, after 23 years of service at NECSA, Jaco relocated to the Netherlands to take up a position as process engineer with the Nuclear Research and Consultancy Group (NRG).

FIGURE 4.—*Xerophyta adendorffii*: a, plants showing abundant flowering about seven days after a rain shower – note thick layer of accumulated dead plant material below plants, indicative of a great age for the colony; b, flowers; c, inferior ovary and pedicel covered with numerous capitate to subsessile glands which extend onto the adjacent dorsal surface of the outer tepals; d, mature basally dehisced capsule crowned with persistent dried remains of the perianth. Scale lines: a, 30 mm; b, 10 mm; c, 2 mm; d, 5 mm. Photographs: a, J. Hyde-Johnson; b–d, A.E. van Wyk.

In general facies, *Xerophyta adendorffii* and *X. schlechteri* are rather similar and sometimes difficult to distinguish from one another. Both are mat-forming (Figures 3a, 4a) with very short (rarely exceeding 10 mm) stems, the leaf blades are persistent, V-shaped, more or less viscid all over due to secretions from mainly sunken but also patelliform (sensu Behnke et al. 2013) glands, and with non-revolute margins. The flowers are predominantly white (Figure 4b), with the inner whorl obtuse. However, an analysis of the *rbcL* gene supports the recognition of *X. adendorffii* as a distinct species (Behnke et al. 2013). Furthermore, this molecular evidence suggests that *X. schlechteri* is more closely related to *X. rehmannii* and *X. rosea*, than to *X. adendorffii*. All of this implies that in a sense *X. adendorffii* is a cryptic species (Chenuil et al. 2019), although some morphological differences to distinguish it from *X. schlechteri* do exist (see next paragraph).

Xerophyta adendorffii differs from *X. schlechteri* in that plants are smaller and more slender (vs. larger and more robust); leaves are somewhat falcate, the distal part often spirally twisted when dry (vs. neither falcate nor twisted); outer tepals usually heavier flushed with purple (vs. mainly white, or if flushed with purple, then only slightly so) and cuspidate (vs. apiculate); and the stigma clearly longer than the style (vs. not obviously so). According to Behnke et al. (2013) the tepals are 15–20 mm long in *X. adendorffii*, but these measurements do not appear to be representative for the species. In the material of *X. adendorffii* examined by us, the tepals were 20–30(–35) mm long, thus overlapping with the length given by Behnke et al. (2013) for *X. schlechteri* (20–25 mm). These greater dimensions for *X. adendorffii* are supported by the size of the well-pressed dried flowers on the paratype, *Adendorff 38* (M-0217875), which have the tepals at least 28 mm long in the dried state. Flower size in *X. adendorffii* does, however, vary depending on the type of flowering event (J.D. Adendorff pers. com.). Flowers tend to be smaller during mass flowering (Figure 4a) following a dry spell (probably due to a greater demand on resources), compared to sparsely produced flowers at other times. In Gauteng *X. schlechteri* has, despite extensive searches (J.D. Adendorff pers. com.), not been recollected since the type gathering was made by Rudolf Schlechter near Donkerhoek, east of Pretoria on 4 January 1894. *Xerophyta viscosa*, with which these two species were previously confused, has stems that are up to 50 mm long and clothed with leaf sheaths, leaf blades that are deciduous and flowers that are bright pinkish red to violet. It has a wide distribution in the eastern parts of South Africa (Eastern Cape, KwaZulu-Natal, Free State provinces), Lesotho and Eswatini (formerly Swaziland).

As was the case in earlier taxonomic studies on *Xerophyta* (e.g. Ayensu 1969), Behnke et al. (2013) found leaf anatomy to be of particular taxonomic significance in the group. *Xerophyta adendorffii* has the basic *Vellozia* Type (VT) of leaf anatomy, a feature shared with *X. schlechteri*, *X. viscosa* and most other species of the Herb Group. This type of anatomy is characterised by leaf blades with grooves on the abaxial surface only (but shallow grooves present adaxially above veins in the desiccated state), no sclerenchyma strands or bands outside vascular bundles, and aquiferous cells restricted to the adaxial groove located above the central vascular bundle (Behnke et al. 2013). Noteworthy, is the presence of resin glands, in the case of *X. adendorffii* superficially on adaxial surface (patelliform glands) or deeply embedded in the palisade tissue of the leaf blade (not to be confused with capitate or near sessile glands associated with the flowers as depicted in Figure 4c), which is the source of the glutinous/viscid secretions covering the leaves of this and other members of

the Herb Group. Although not described in any detail in *X. adendorffii*, the structure of these glands are probably very similar to what has been elucidated in the related *X. seinei* (Behnke et al. 2002) and *X. viscosa* (Naidoo et al. 2009).

Information on the chemical composition of the glutinous leaf secretions in *Xerophyta viscosa* are provided by Naidoo et al. (2009). Possible functions of these secretions in *Xerophyta* and other Velloziaceae are largely speculative, but include ultraviolet screening, protection against water loss and high temperatures, and defences against herbivores, insects and pathogens (Naidoo et al. 2009; Martins & Paiva 2016). Some species of *Vellozia* in Latin America are highly flammable due to the presence of resin in all parts of the plants (Kubitzki 1998). Based on this property and a study of the resin composition in *V. variabilis*, Martins & Paiva (2016) suggested that in addition to other possible survival functions, the flammable resin of *V. variabilis* safeguards the plant's meristem from fire damage by facilitating the rapid burning of the plant and, thus, protecting the plant's fire-sensitive tissues. It remains to be established if the glutinous leaf surface secretions in *Xerophyta* are similarly enhancing the selective flammability of different parts of plants. Also, nothing is known about the composition and function of the blackish secretions of the capitate glands associated with the flowers (Figure 4c).

The specimens of *Xerophyta adendorffii* figured here were collected on chert-impregnated dolomite outcrops at Kalkheuvel West (Gauteng) near Broederstroom (North West), South Africa. This is close to the type locality, which is about 5 km south of Broederstroom, on slopes west of the Crocodile River, along the Road 512 from Broederstroom to Lanseria. The extensive dolomitic area in and around Kalkheuvel West harbours a rich flora with some rare species and unusual vegetation types. Particularly noteworthy is the so-called 'silver vegetation', a plant community of which the foliage of several woody species have a silver-grey colour (Krige & Van Wyk 2005).

At Kalkheuvel West, *Xerophyta adendorffii* grows as dense mats in shallow soil associated with dolomite/chert outcrops (Figure 3a). Older tussocks/clumps die from the centre while expanding by the formation of new plantlets along the periphery. Judging from the, mainly dead, thick layers of accumulated old plant material below these mats (Figure 4a), some colonies must be very old, perhaps several centuries. The plants are usually rooted in rock fissures (so-called chasmophytes) and prefer open areas with full sunlight. In this xeric habitat, the species is often associated with dwarf and tall forms of *X. retinervis*. Species of Velloziaceae in Brazil have an array of root specialisations to exploit nutrient-poor habitats. Certain members of *Barbacenia* endemic to phosphorous-poor rocky habitats in the *campos rupestres* (rocky outcrops dominated by fire-prone grassland) of Brazil's dry interior have specialised roots that penetrate quartzite (Teodoro et al. 2019). These so-called vellozioid roots secrete acids that dissolve the rock, allowing phosphorous extraction by the plant, and increasing rock porosity and water retention. In this way, the plants actively contribute to the weathering of rocks and soil formation (Abrahão et al. 2020). The Herb Group species of *Xerophyta* generally exploit habitats similar to those of their South American relatives, prompting the question whether similar root adaptations exist in local species. This may well be the case because in *X. adendorffii* we have noticed sections of roots densely covered in what appears to be unusually long root hairs, one of the morphological features characterising vellozioid roots (Teodoro et al. 2019).

Following field observations, it can be confirmed that *Xerophyta adendorffii* shows typical desiccation-tolerant behaviour, in other words, it is a resurrection plant (Figure 3). Desiccation tolerance is defined as the ability of a plant to sustain loss of up to 95% of its water content, to remain in the dry state for a prolonged period of time, and to revive full metabolic activity within hours to days following wetting (Gaff 1977). During prolonged dry spells, desiccated leaves of *X. adendorffii* are tightly folded upwards along the central vascular bundle (midrib), with only the lower surface being exposed to the light. Upon wetting the leaves take up water, the blade (except for the terminal portion) expands and fully unfolds within about two hours. Following desiccation, however, the terminal portions suffer cellular death (senescence) and do not revive. With each desiccation event, a little more tissue from the apex of the leaves does not recover (reminiscent of the state in *X. schlechteri*, as reported by Radermacher et al. 2019). Dead leaf tips and older leaves can be distinguished by their pale grey colour. Initially the rehydrated leaves are usually yellow or sometimes reddish (especially in winter), but they soon change to green (see further on). During drought-induced desiccation the leaves change from green to yellow (Figure 3c), becoming reddish brown to blackish (almost appearing as if scorched) when fully shrivelled and dormant.

Winters in the species' habitat are usually dry and quite cold with occasional frost. Following an unseasonal heavy rain shower during a cold June in 2020, plants revived to assume a mostly dark reddish-maroon colour (Figure 3b) before turning green after about seven days. Such a predominantly reddish appearance has not been observed during revival of the plants in summer; then the leaves are usually yellowish (Figure 3c) before greening, hence we suspect cold stress may have contributed to this colour change. The reddish pigment was mainly confined to the epidermis of the leaf blades, whereas the mesophyll was green. Based on studies on other groups of plants, we have assumed that the reddish to purplish pigmentation in *Xerophyta adendorffii* is caused by anthocyanins. The superficial location of the pigment suggests an adaptive role as a type of light filter. Most popular is the so-called photo-protection hypothesis, which suggests that the red pigments protect against the harmful effects of light (Archetti et al. 2009). During photosynthesis, continuous damage occurs to photosystem II in the chloroplast and this requires constant repair. If the light intensity is very high, and especially under certain stressful environmental conditions such as drought and cold, the rate of damage exceeds the rate of repair. This leads to long-term damage to the photosynthetic apparatus in the chloroplast, termed photoinhibition. There is substantial experimental evidence that foliar anthocyanins serve as a sunblock, protecting chloroplasts from the adverse effects of excess light (Landi et al. 2015, and references therein). The accumulation of anthocyanins during dehydration of *X. viscosa* and *X. schlechteri* leaves has also been suggested as providing protection at the level of light absorption (e.g. Sherwin & Farrant 1998; Radermacher et al. 2019).

Desiccation-tolerant (DT) plants can be divided into two main groups (Tuba & Lichtenthaler 2011), namely those which normally retain their chlorophyll upon drying, referred to as homoiochlorophyllous (HDT) plants, and those which lose their chlorophyll (but retain some yellow carotenoids) content during desiccation, known as poikilochlorophyllous (PDT) plants. HDT plants retain most or part of their chlorophyll and photosynthetic complement in the dry state, and rely on various mechanisms to protect themselves against photo-oxidative damage. Such species revive very quickly by being green from the

onset following rehydration. In PDT plants, on the other hand, chlorophyll must be resynthesised following remoistening, a process that can take several hours for normal levels of chlorophyll and carotenoids to be restored. *Xerophyta adendorffii* is clearly a PDT plant and upon rehydration its leaves gradually change from yellow (sometimes reddish, especially under frosty/cold conditions in winter) to green over a period of one to three days (Figure 3). The selective advantage of PDT is believed to be the minimising of photo-oxidative damage and not having to maintain an intact photosynthetic system through long (up to ten months in some species) inactive periods of desiccation (Tuba 2008). Hitherto PDT has only been recorded in monocots, with Velloziaceae the largest family of desiccation-tolerant angiosperms (Porembski 2011).

FIGURE 5.—A hoverfly (Syrphidae) visiting a flower of *Xerophyta adendorffii*; these insects were frequently noted on flowers of this species and, in addition to honeybees, are suspected to be one of the pollinators. Photograph: J. Hyde-Johnson.

Pioneering studies on the physiology of revival following desiccation in *Xerophyta* were conducted by the late Prof. Zoltán Tuba (Hungary) and co-workers on a taxon referred to as *Xerophyta scabrida*, a member of the Shrub Group, which has subsequently served as a model plant for PDT (e.g. Tuba et al. 1994; for a summary of the mechanisms involved, see Tuba & Lichtenthaler 2011). Much of Tuba's research was based on plants from Mindu Hill, Uluguru Mountains, Tanzania. According to the new classification of Behnke et al. (2013), true *X. scabrida* is only known from Angola and the Democratic Republic of Congo. Thus, the correct name for the taxon referred to as *X. scabrida* in these PDT studies is *X. tanzaniana*, a newly recognised species native to Tanzania and Mozambique. The mechanism of PDT has also been exhaustively studied by other research teams in three species of the Herb Group, namely *X. viscosa*, *X. humilis* and *X. schlechteri* (e.g. Lüttge et al. 2011; Radermacher et al. 2019).

Although the odd flower may be found on plants of *Xerophyta adendorffii* at any time during summer and autumn (November–May), flushes of flowers (Figure 4a) are invariably produced about four to seven days after a good rainfall event that follows a period of drought (not necessary desiccation). This may happen several times during the main rainy season (summer). The open flowers have a pleasant scent and amongst the potential pollinators visiting them were honeybees (*Apis mellifera scutellata*) and hoverflies (Syrphidae; Figure 5) (own observations and J.D. Adendorff pers. com.). As is the case in other species of *Xerophyta*, the flowers of *X. adendorffii*, mostly the tepals, are heavily fed on by beetles of the families Chrysomelidae and Meloidae, particularly blister beetles (*Hycleus* spp.) (J.D. Adendorff pers. com.). At Kalkheuvel West the still developing fruit are eaten by caterpillars of the polyphagous African boll worm moth (*Helicoverpa armigera*; Figure 6) and the larva of another, as yet unidentified, lepidopteran. As they ripen, the fruit are inverted about 90° on the pedicels and when mature, the capsules dehisce by means of three slits at the base

FIGURE 6.—Developing fruit of *Xerophyta adendorffii* being eaten by a caterpillar of the polyphagous African boll worm moth (*Helicoverpa armigera*). Photograph: J. Hyde-Johnson.

to resemble a basket opened at the top (Figure 4d). We have noticed the developing ovaries and green capsules being selectively eaten at night by a larger animal, most probably a rodent.

No recorded past or present uses by humans could be found for *Xerophyta adendorffii*, and if there have been any in the past, that knowledge has most probably been lost. It is reasonable to expect though that it would have had potentially similar uses to other species in the Dwarf Group, but again, very little published information exists for those species. In this regard, we do know that formerly the fibrous leaves of *X. viscosa* have been plaited into rope (Pooley 1998, Moffett 2010). This lack of biocultural information, however, does not mean that it's not worth investigating *X. adendorffii* further. The chemistry of Velloziaceae is still comparatively poorly known. The family is particularly rich in surface lipophilic flavonoids, the composition and distribution of which are taxonomically significant (Harborne & Williams 1994 and references therein). Because of their specialised physiology, resurrection plants in general are rich sources of primary and secondary metabolites, thus rendering them possible candidates for the development of novel drug substances as well as for cosmetics (Gechev et al. 2014). Moreover, in a sense the genetic basis for extreme drought tolerance in resurrection plants is a form of 'natural capital', as highlighted by Grace (2019) for succulent plants. In fact, studies to unravel the molecular and physiological adaptations of drought-tolerance in the model species, *X. humilis*, *X. schlechteri* (referred to as *X. viscosa* in earlier papers involving study material from Buffelskloof Private Nature Reserve, Mpumalanga, South Africa) and *X. viscosa*, with the view to eventually transfer some of these to crop plants, are already in progress (e.g. Hillhorst & Farrant 2018; Radermacher et al. 2019).

In the Red List of South African Plants, *Xerophyta adendorffii* is listed as Vulnerable (Von Staden 2014). It is placed in this category mainly because of its very localised distribution and small extent of occurrence. The population of the species is declining due to ongoing habitat loss and degradation. Habitat loss is mainly attributable to residential development in the greater Hartbeespoort Dam area. Although perhaps the bulk part of its distribution range falls (Figure 2) within protected areas and conservancies, including the Magaliesberg Biosphere Region and Cradle of Humankind World Heritage Site, in many of these the habitat is being transformed, mainly by bush encroachment. This increase in the density of

woody plants is brought about by inappropriate management practices, notably overgrazing and the suppression of fire. Regular burning of the vegetation in this ecotonal area between grassland and savanna biomes is essential for the maintenance of the ecosystem (Van Wyk 2012). Competition from alien invasive plants is an additional, minor threat.

Besides curiosity value as a resurrection plant, there is not much on which to promote *Xerophyta adendorffii* as an ornamental. In any case, some of the more attractive Shrub Group species of *Xerophyta* are extremely slow-growing and notoriously difficult to maintain in cultivation. This is the main reason why these plants are rarely encountered in gardens, and then mostly as confiscated mature plants illegally gathered from the wild and replanted in botanical gardens. According to Nichols (2005), the best way to propagate South African species of Velloziaceae is from seed. Freshly collected seeds are sown in trays and watered from below. Seed germinate in 2–4 weeks with the seedlings left in the trays for a season to get root-bound. Seedlings can then be transplanted in shallow soil (e.g. a shallow container) to imitate the rock plates of their natural habitat. Although nothing is known about the cultivation of *X. adendorffii*, related Herb Group species transplanted from nature to greenhouses for scientific study do survive, at least in the short term (Sherwin & Farrant 1996; Behnke et al. 2002; Collett et al. 2004; Radermacher et al. 2019). Plants of *X. viscosa*, *X. humilis* and *X. schlechteri* were grown in a mixture of peat, river sand and potting soil and were maintained in a greenhouse with no supplementary lighting, *X. viscosa* under 30% shade cloth, the other two without shading. To maintain the hardiness of the plants, they were subject to regular cycles of desiccation and rewatering.

Description.—Perennial tufted herbs, proliferating outwards to form dense mats. *Stems* indistinct or very short, rarely exceeding 10 mm in length. *Leaves* tristichous, bright-green, yellow or reddish depending on stage of desiccation/rehydration, 50–130(–200) mm long, 4–7 mm wide; blades persistent, V-shaped with prominent keel, but progressively conduplicate distally, falcate with an acuminate tip, moderately viscid, notably above, adaxially often with slightly raised humps of resins reflecting position of embedded and patelliform resin glands, abaxially shallowly longitudinally grooved amongst veins, margins and keel distinctly serrulate (Figure 2f), the teeth pointing towards leaf apex, distal portion often dead, dry leaves folded upwards along midvein and partly spirally twisted. *Flowers* borne apically, bisexual, regular, solitary, infundibular, 22–35 mm in diameter when open; pedicel (25–)50–90(–100) mm long, ± 1 mm in diameter, green, often purple-flushed, with numerous dark capitate glands, the density increasing towards the flower. *Tepals* 3 + 3, petaloid, ± lanceolate, free, (15–)20–30(–35) mm long, white, variously purple-flushed; outer series 4–5 mm wide, ventrally white and usually slightly purple-flushed, eglandular, dorsally pale to dark purple with capitate glands at least proximally, apices cuspidate; inner series 5–7 mm wide, white, glabrous, apices obtuse. *Stamens* 3 + 3, inserted at base of perianth; filaments 1–2 mm long; anthers basifixed, erect, 7–10 mm long, opening from the top by longitudinal slits, outer series narrower, ± 0.25 mm wide, inner series broader, ± 0.5 mm wide; pollen grains shed as monads, yellow. *Ovary* inferior, almost globose, 3-locular, ± 6 × 5 mm, densely covered with dark capitate to subsessile glands which extend onto the dorsal surface of the outer tepals; ovules many per locule, with axile placentation on intrusive placentas. *Style* 3–5 mm long, ± 0.6 mm in diameter, stigma columnar, tapering towards apex, longitudinally 3-grooved (stigmatoid bands), 7–12 mm long, ± 1.5 mm in diameter. *Fruit* a capsule, inverted when ripe, crowned with dried remains of the perianth,

loculicidally dehiscent at the base. *Seeds* many, ± attenuate-turbinate, angled, ± 0.8–1.2 mm long, light brown. Plate 2361.

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PLATE 2362 *Aloiampelos ciliaris* var. *ciliaris*

Aloiampelos ciliaris var. *ciliaris* Asphodelaceae: Alooideae

South Africa

Aloiampelos ciliaris *(Haw.) Klopper & Gideon F.Sm*. var. **ciliaris** in Phytotaxa 76: 10 (2013); Smith et al.: 153 (2017). *Aloe ciliaris* Haw.: 281 (1825); Salm-Dyck: sect. 25, Fig. 1 (1837); Baker: 169 (1880); Baker: 317 (1896); Berger: 255 (1908); Marloth: 95, t. 23 (1915); Groenewald: 41 (1941); Reynolds: 352 (1950); Jacobsen: 156 (1960); Jeppe: 110 (1969); Bornman & Hardy: 191 (1971); Jacobsen: 75 (1974); Hunt: t. 763 (1978); Van Wyk & Smith: 94 (1996); Glen & Hardy: 93 (2000); Newton: 129 (2001a); Newton: 122 (2001b); Van Wyk & Smith: 98 (2003); Smith & Van Wyk: 69 (2008); Carter et al.: 540 (2011); Grace et al.: 36 (2011); Van Wyk & Smith: 108 (2014); Klopper: 175 (2015); Newton: 532 (2020). *Aloe ciliaris* var. *flanaganii* Schönland: 42 (1903). *Aloe ciliaris* f. *flanaganii* (Schönland) Resende: 101 (1943). *Aloe ciliaris* f. *haworthii* Resende: 101 (1943).

The genus *Aloiampelos* Klopper & Gideon F.Sm. was established in 2013 to accommodate *Aloe* sect. *Macrifoliae* (Haw.) Glen & D.S.Hardy, as part of a revised generic classification for *Aloe* L. *sensu lato*, based on results from molecular phylogenetic research (Grace et al. 2013). The name is derived from the Greek word *ampelos* (a climbing plant) and the word *aloe*, and alludes to the general climbing habit of these aloes. The genus comprises seven species (one with three varieties and a nothovariety, and another with two varieties), all of which are endemic to South Africa. Members of this genus occur mostly in the Western and Eastern Cape provinces, often close to the coast, but some are also present at higher altitudes inland, near the Free State–Lesotho border (*A. striatula* (Haw.) Klopper & Gideon F.Sm. var. *striatula*) or as far northeast as the KwaZulu-Natal border with Eswatini (*A. tenuior* (Haw.) Klopper & Gideon F.Sm.). These aloes are known as rambling or scrambling aloes and are generally characterised by their creeping, shrubby, or climbing habit. The rather narrow, thin leaves are spirally arranged along slender stems and are separated by prominent internodes, thus displaying a distinct sheathing base. The usually unbranched inflorescences can be either lax to subdense (Figure 1) and cylindrical, or densely near-capitate (Figure 2), and carry rather small to medium-sized, cylindrical flowers that range from yellow through orange to red. Rambling aloes occur in the winter, summer, and year-round rainfall regions in a variety of habitats where they are most often found in the ecotone between vegetation types (Ellis 2013; Klopper & Smith 2017).

Other rambling aloes that have been illustrated in this series are *Aloiampelos gracilis* (Haw.) Klopper & Gideon F.Sm. as *Aloe laxiflora* N.E.Br. (Pole Evans 1928), *Aloiampelos ciliaris* var. *tidmarshii* (Schönland) Klopper & Gideon F.Sm. as *Aloe tidmarshii* (Schönland) F.S.Mull. ex R.A.Dyer (Dyer 1943) and *Aloiampelos tenuior* as *Aloe tenuior* Haw. (Verdoorn 1961). *Aloiampelos striatula* var. *caesia* (Reynolds) Klopper & Gideon F.Sm. was also first described in this journal, as *Aloe striatula* var. *caesia* Reynolds (Reynolds 1936).

In terms of evolutionary relationships, the consensus phylogenetic tree of Asphodelaceae subfamily Alooideae produced by Daru et al. (2013) establishes *Aloiampelos* as a

PLATE 2362.—1, terminal portion of a leafy stem, × 1; 2, inflorescence, × 0.75; 3, single flower, × 1. Voucher specimen: *G.F. Smith & E. Figueiredo 62* in H.G.W.J. Schweickerdt Herbarium, Pretoria. Artist: Gillian Condy.

FIGURE 1.—Most forms of *Aloiampelos ciliaris* var. *ciliaris* are characterised by having short, densely flowered inflorescences. However, this character shows some variation with other forms having more laxly flowered, elongated inflorescences, as here. Photograph: G.F. Smith.

well-supported clade in which *A. ciliaris* is sister to *A. tenuior*. This species pair is most closely related to *A. striatula*, with *Aloiampelos gracilis* and *A. commixta* (A.Berger) Klopper & Gideon F.Sm. slightly less closely related. *Aloiampelos decumbens* (Reynolds) Klopper & Gideon F.Sm. and *A. juddii* (Van Jaarsv.) Klopper & Gideon F.Sm. were omitted from this study, so we do not yet know how these fit into the phylogeny of *Aloiampelos*.

Aloiampelos ciliaris was described by the English botanist Adrian Hardy Haworth (19 April 1767–24 August 1833) in 1825 (as *Aloe ciliaris*) based on material sent to England from South Africa by James Bowie (ca. 1789–1869). Bowie was documented (Gunn & Codd 1981) to make two botanical collecting journeys into the Eastern Cape region, the first between September 1820 and January 1821 and the second from June 1821 into the early months of 1822. Based on his routes (Smith & Van Wyk 1989) he could reasonably have collected his material of *Aloiampelos ciliaris* during either of these excursions. However, Reynolds (1950) states that 'it appears that Burchell was the first to collect a specimen of this species on 9 October 1813 between Riet Fontein and the Kowie River, near Port Alfred, in the Bathhurst Division. According to Baker, this specimen (*Burchell 3993* in Herb. Kew) is *A. ciliaris*'. Principally due to its unusual characteristic of being the only hexaploid ($2n = 42$) alooid species in South Africa *A. ciliaris* has been subject to several studies (e.g. Müller 1945; Brandham 1971; Riley & Majumdar 1979; Brandham & Carter 1990). This uniquely high chromosome count for a South African alooid was first reported by Ferguson (1926), but the count was then given imprecisely as $2n > 45$.

Apart from the typical variety, two further varieties are currently recognised in *Aloiampelos ciliaris*, namely the tetraploid *A. ciliaris* var. *redacta* (S.Carter) Klopper & Gideon F.Sm. (in Grace et al. 2013) and the diploid *A. ciliaris* var. *tidmarshii* (Schönland) Klopper & Gideon F.Sm. (in Grace et al. 2013). Apart from chromosome numbers, these varieties are distinguished on morphological grounds, namely raceme density, dimensions of the leaves and flowers, and the size of the cilia on the leaf margins and adjacent amplexicaul leaf bases (Figure 3).

In the 1930s and 1940s the Portuguese botanist Flávio Ferreira Pinto Resende (28 February 1907–1 January 1967), who was attached to the University of Lisbon at the time,

had more than a passing interest in the taxonomy of southern African Asphodelaceae subfam. Alooideae, including *Aloiampelos*, which was then widely treated as belonging to *Aloe* § *Macrifoliae* (Fernandes 1967; Lima de Faria 1967; Figueiredo et al. 2019; Smith & Silva 2019; Smith et al. 2020). Resende inter alia published a number of names for formae in *Aloiampelos ciliaris*, all of which were based on minor morphological variations, and until recently none of these names were upheld. *Aloe ciliaris* f. *gigas* Resende, which Resende (1938) encountered in cultivation, was described as a pentaploid ($2n = 35$), and we therefore deliberately do not here place it in the synonymy of *Aloiampelos ciliaris* var. *ciliaris* (see Resende 1938, 1940). *Aloe ciliaris* f. *gigas* was later interpreted by Brandham & Carter (1990) as a possible natural hybrid between the tetraploid (*A. ciliaris* var. *redacta*) and hexaploid (*A. ciliaris* var. *ciliaris*) varieties. Smith & Figueiredo (2019) raised *Aloe ciliaris* f. *gigas* to the rank of nothovariety, as *Aloiampelos ciliaris* nothovar. *gigas* (Resende) Gideon F.Sm. & Figueiredo, given that Resende (1938, 1943) encountered the plants he described as *Aloe ciliaris* f. *gigas* in the Jardim Botânico de Coimbra, in 1937. A new combination and status for *Aloe ciliaris* f. *gigas* under *Aloiampelos ciliaris* as a nothovariety, and not a variety, was therefore preferred.

FIGURE 2.—This form of *Aloiampelos ciliaris* var. *ciliaris* has short, densely flowered racemes. Photograph: N.R. Crouch.

FIGURE 3.—The amplexicaul portion of the leaf bases of *Aloiampelos ciliaris* var. *ciliaris* are adorned with conspicuous, white cilia. Photograph: G.F. Smith.

When Haworth (1825) established the basionym *Aloe ciliaris*, he stated that plants of the species he was describing had been found by 'Mr. Bowie; who safely transmitted them to […] Kew, where they are now flourishing'. In the description of the species Haworth stated that 'caudex nunc 3–5-pedalis apud Kew', meaning that the plant was then growing at Kew and had reached a height of 1.0–1.5 m. It is not known if Haworth obtained Bowie-collected herbarium specimens from Kew or if he described the plant based only on material that was cultivated there. The description is very brief and deals with vegetative characters only.

After Haworth died, his herbarium was bought by the English botanist Henry Borron Fielding (1805–1851). Fielding used this herbarium for study and most specimens were

thrown away (Clokie 1964). What remained of Haworth's herbarium was later bequeathed to the University of Oxford, together with the rest of Fielding's herbarium. It is now kept at OXF (Fielding-Druce Herbarium). There are no specimens of *Aloiampelos ciliaris* among the collections originating with Haworth (S.K. Marner pers. comm.). The specimen grown at Kew and described by Haworth does not appear to have been preserved in Herb. K either.

The Royal Botanic Gardens, Kew, hold an early illustration of *Aloiampelos ciliaris* (Figure 4) in their Art Collections section (P. Long, pers. comm.). The plate is undated and was executed ['del.'] by Thomas Duncanson (Hunt 1989; Blunt & Stearn 1994), and is of sterile material (a leafy stem only) (Figure 3). The name written in ink at the bottom of the painting reads: 'Aloe ciliaris. Haw.', and below it is written '(Provisional)' in a different hand using different writing material (pencil?). The name and the word below it seem to have been written at different times. On a strip of paper attached to the plate base is written: 'Received from Mr [James] Bowie in the year 1821 from the Cape of Good Hope.' A determinavit strip dated 11 Oct. 1989 and signed by S. Carter was affixed to the painting and states: 'In the absence of herbarium material, this painting becomes the HOLOTYPE of Aloe ciliaris Haworth. in Phil. Mag. et Journ. 66: 281 (1825)'. The plate does not carry any further numbers or annotations. However, this plate cannot be the holotype as it was not cited by Haworth (1825), and there is no evidence that it was 'the **one** [emphasis by present authors] specimen or illustration […] either *(a)* indicated by the author(s) as the nomenclatural type or *(b)* used by the author(s) when no type was indicated' (Turland et al. 2018: 19–20, Article 9.1).

The type (holotype, lectotype or neotype) of a name of a species or infraspecific taxon is either a single specimen conserved in one herbarium or other collection or institution, or an illustration (Turland et al. 2018: 16, Article 8.1). Further, Article 9.4 of the *Code* states that a lectotype is a specimen or illustration designated from the **original material** [emphasis by present authors] as the nomenclatural type, if no holotype was indicated at the time of publication. Under the Shenzhen *Code* (Turland et al. 2018) original material includes elements 'that the author associated with the taxon, and that were available to the author prior to, or at the time of, preparation of the description'. The Kew plate undoubtedly depicts the material that was dispatched to England, and the plate would have been available to Haworth by 1825; this is the material described by Haworth as *Aloe ciliaris*. The type status of the plate is here amended to that of lectotype, as it cannot be the holotype. It was designated by Glen & Hardy (2000) as 'iconotype', a term that has no standing under the *Code*. Until recently it had to be shown that the validating description or diagnosis was based on certain specimens or illustrations in order for them to qualify as original material, but this is no longer required. The present *Code* (Turland et al. 2018 in Article 9.4(d)) allows for duplicates of type material (isotypes or isosyntypes) that were not seen by the author to be considered as original material. Nevertheless, in this case, indications are that the plate represents the material on which the description was based and therefore the illustration, although unpublished and uncited, can be considered as associated with the taxon by the author (Article 9.4(a)).

Aloiampelos ciliaris var. *ciliaris* occurs naturally in the Eastern Cape Province of South Africa (Figure 5) where it is a component of sparse to very dense thicket vegetation in the

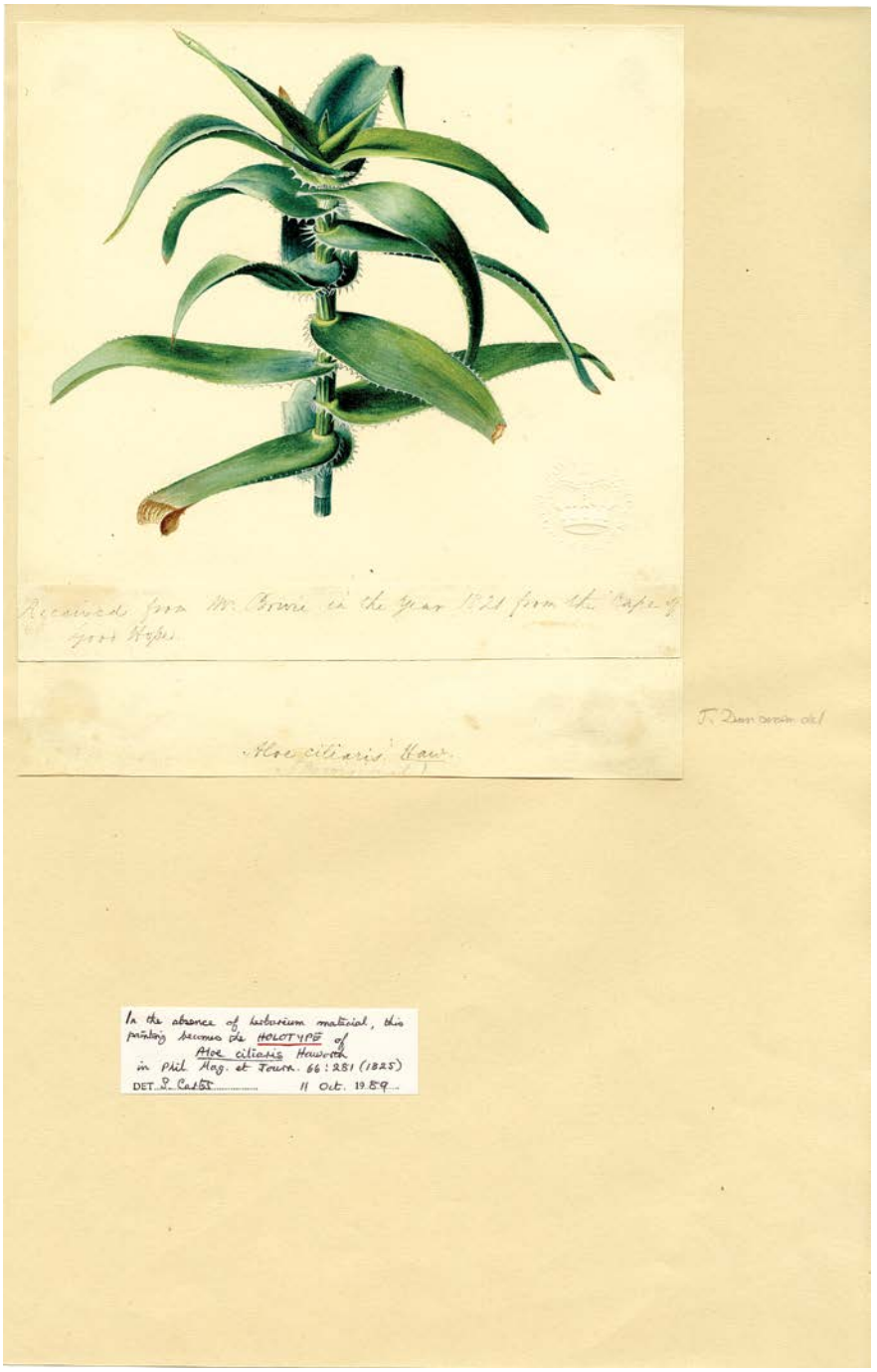

FIGURE 4.—Image of the lectotype of the name *Aloiampelos ciliaris*. This illustration by Thomas Duncanson is inscribed: 'Received from Mr [James] Bowie in the year 1821 from the Cape of Good Hope.' Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.

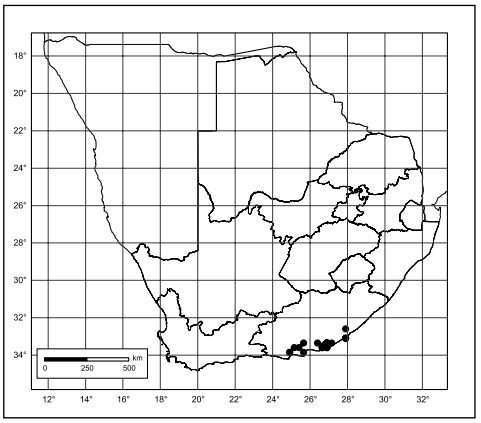

FIGURE 5.—Known geographical distribution range of *Aloiampelos ciliaris* var. *ciliaris* in southern Africa.

FIGURE 6.—When subjected to significant water stress during the flowering season, *Aloiampelos ciliaris* has a tendency to self-prune flowers from its inflorescences. Photograph: G.F. Smith.

Maputaland–Pondoland Region of Endemism (Van Wyk & Smith 2001). Interestingly, the species reportedly also occurs on Mount Kulal in northern Kenya, several thousand kilometres further north from its Eastern Cape range (Hunt 1978). We have been unable to confirm the natural occurrence of the species at this east-central African locality, where Hunt (1978) stated it to not have been a garden escape, the most likely explanation for this discontinuity. Notably there is a village on Mount Kulal, where several expatriates have lived, and it seems likely that this plant was cultivated there, as it is in Nairobi, and became a garden escape (L.E. Newton pers. comm.).

Like the other taxa of *Aloiampelos*, for example *A. tenuior* and *A. ciliaris* var. *tidmarshii*, from the central and eastern parts of the Eastern Cape of South Africa, *A. ciliaris* var. *ciliaris* is very easy in cultivation in southern Africa and some parts of the northern hemisphere. Propagation is through cuttings about 200–500 mm long that require no special treatment. Such cuttings, of which the cut ends have been allowed to dry for a few days in a shady position, can be established directly in the place that they are intended to grow. Plants are tolerant of a wide range of soil types, ranging from rather heavy clays to light, sandy soils. They do especially well when the soil is enriched with thick layers of compost; in their natural thicket habitats considerable leaf-fall collects under the canopies of the small to medium-sized trees into which they scramble. *Aloiampelos ciliaris*, including the varieties and nothovariety recognised in it, is one of the few aloe species that will self-prune flowers from its congested or slightly elongated inflorescences when under water stress (Figure 6). Accordingly, to ensure full and attractive inflorescences, plants should not be allowed to dry out completely during the flowering season.

The subject of this account could be confused with other genus members, especially *Aloiampelos tenuior*, which may also present red flowers with yellow tips. However, the prominent cilia that fringe the sheathing bases of the leaves of *A. ciliaris* (except in the case of *A. ciliaris* nothovar. *gigas*, Figure 7) is a highly distinctive feature that should settle any concerns about identity. In addition, the flowers of *A. tenuior* are consistently smaller than those of *A. ciliaris* and hardly, if at all, banana-like curved.

FIGURE 7.—The upper margin of the amplexicaul section of the leaves of *Aloiampelos ciliaris* nothovar. *gigas* completely lacks prominent cilia. Photograph taken on 30 September 2014 of material cultivated near Serra de Santo António in central Portugal. Photograph: G.F. Smith.

Aloiampelos ciliaris is a perfect scrambler to train onto a trellis if a dull spot or wall needs to be brightened up with a plant that forms multiple stems. In time, plants tend to topple over so it is best to tie the stems to stakes that can later be removed; as plants elongate the stems can be tied to the trellis. If otherwise left untrained in a garden bed, plants will form a large mass of tangled stems; these are especially striking when in flower (Figures 8 and 9). Once established and growing, the stems of *A. ciliaris* can reach a staggering 5–6 m in length. In cultivation, fruit development and seed-set in *A. ciliaris* var. *ciliaris* depend on the availability of multiple clones of the variety that flower simultaneously. Otherwise, given that *A. ciliaris* var. *ciliaris* is a hexaploid and the majority of widely cultivated aloes are diploid, fruit and seed production is at best erratic (Figure 10), such that germinated seeds almost invariably give rise to tetraploid hybrids.

FIGURE 8.—If *Aloiampelos ciliaris* is left untrained in a garden bed, plants will form large masses of tangled stems; these are especially striking when in flower. Photograph: N.R. Crouch.

In greenhouse or conservatory cultivation in Europe and perhaps elsewhere in the northern hemisphere, this plant can be slightly tricky given that its leaves are not all that succulent. Consequently, it requires modest winter warmth and water to prevent desiccation and death, so we recommend a minimum winter temperature of +10°C so that it can be watered regularly. In contrast, both varieties of *Aloiampelos*

FIGURE 9.—The inflorescences of *Aloiampelos ciliaris* are usually simple, but sometimes a short branch is produced. Photograph: G.F. Smith.

FIGURE 10.—In cultivation, fruit and seed production in *Aloiampelos ciliaris* var. *ciliaris* is erratic, as here, unless multiple clones of this hexaploid variety are flowered together. Photograph: G.F. Smith.

striatula are frost-hardy and have survived outdoor cultivation in England in unheated greenhouses and cold frames for many winters.

Plants of *Aloiampelos ciliaris* can be temperamental when it comes to flowering. Some clones have been observed to skip one or more seasons between flowering events, while others will produce only one or two inflorescences per clump per season. Doubtless through a process of horticultural selection, profuse-flowering forms are commonplace and have become popular in cultivation in mild-climate parts of the world, for example in Mediterranean Europe and along the central and southern Californian coast in the USA (Van Wyk & Smith 1996). *Aloiampelos ciliaris* generally flowers during the late winter (July–August, southern hemisphere), but, like *A. tenuior*, can sporadically flower during any month of the year. The preferred form of *A. ciliaris* that has found favour among gardeners has comparatively short inflorescences and crimson red flowers. However, forms with more elongated racemes and orange-red flowers are also often encountered in cultivation.

Description.—Much-branched, tangled shrub. *Stems* long and slender, up to 5–6 m long, 10–15 mm in diameter, repeatedly branched, scandent, only terminal 0.3–0.6 m with leaves. *Leaves* cauline-dispersed, spreading to recurved, green, without spots, rather thin, linear-lanceolate, long acuminate, 100–150 mm long, 15–25 mm wide; sheath distinctly auriculate with ciliate margin, cilia 2–4 mm long, obscurely green-lineate, 5–15 mm long; margin with firm, white, cartilaginous teeth, ± 1 mm long, ± 3 mm distant. *Inflorescence* 0.2–0.3 m long, ascending, arising laterally below apical leaves, usually simple, sometimes with short branch. *Peduncle* 0.12–0.15 m long, biconvex at base,

with few scattered, deltoid-subulate sterile bracts, ± 5 mm long. *Racemes* broadly cylindric, 80–150 mm long, 40–50 mm wide, erect, subdense to dense; buds spreading, flowers nodding to pendulous when open. *Floral bracts* ovate-acuminate, 4–5 mm long, 1–2 mm wide, white, thin, scarious, 3-nerved. *Pedicels* 5–8 mm long. *Flowers*: perianth orange to orange-red to scarlet red with yellowish green tips, 28–35 mm long, ± 5 mm across ovary, enlarging slightly to ± 7 mm towards mouth, slightly clavate or cylindric; outer segments free for 6 mm, tips straight or slightly incurved; stamens with filiform-flattened filaments, exserted 2–4 mm; ovary 4 mm long, 2 mm in diameter, pale green; style exserted 3–4 mm. *Fruit* an erect, dull green, apically truncate, loculicidally dehiscing, cylindrical to nearly round, trilocular capsule, (13–)15(–18) mm long, (8–)9–11(–13) mm in diameter, desiccating tepals remaining attached to fruit for a long time, chartaceous to slightly woody and transversely ridged when dry, apically valves sigmoidally curved outwards. *Seeds* dark greyish brown to black, irregularly angled, laterally somewhat compressed, 5–7 mm long, with up to 1 mm wide yellowish brown wing stretching around part of periphery of seed. *Chromosome number*: $2n = 42$ (hexaploid). Plate 2362.

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PLATE 2363 *Aloiampelos tenuior* var. *viridifolia*

Aloiampelos tenuior var. *viridifolia* Asphodelaceae

South Africa

Aloiampelos tenuior *(Haw.) Klopper & Gideon F.Sm.* var. **viridifolia** *(Van Jaarsv.) Van Jaarsv.,* comb. nov.

Basionym: *Aloe tenuior* var. *viridifolia* Van Jaarsv. (*Aloe* 44,3: 60, 2007). TYPE.—SOUTH AFRICA. Eastern Cape Province, Kabouga, 3325 (Kirkwood): Rocky outcrop, south-east facing sandstone ridge, (–AD), *Van Jaarsveld, Voigt & Bayer 17832* (NBG, holo.).

Aloe is a very large and morphologically diverse group within the family Asphodelaceae and one of 14 families within the order Aparagales. The Asphodelaceae is a diverse family consisting of 39 genera and about 1 200 species (Christenhusz 2017), divided into three subfamilies, Asphodeloideae, Xanthorrhoeoideae and Hemerocallidoideae, of which the Asphodeloideae is the largest (18 genera and more than 1 000 species). Within the Asphodeloideae *Aloe*, with its mainly African distribution (Reynolds 1950; Carter et al. 2011; Grace et al. 2011), is the largest genus. The restructuring of the large genus *Aloe*, following DNA investigations by Grace et al. (2013), resulted in seven newly created genera: *Aloiampelos* Klopper & Gideon F.Sm. (to which our taxon belongs), *Aloidendron* (A.Berger) Klopper & Gideon F.Sm., *Aristaloe* Boatwr. & J.C.Manning, *Gonialoe* (L.) Boatwr. & J.C.Manning, *Haworthiopsis* G.D.Rowley, *Tulista* Raf. and *Kumara* Medik. (Manning et al. 2014). The latter two genera were the result of older valid names that were resurrected.

Aloiampelos was created by Klopper and Smith (Grace et al. 2013) to accommodate the very distinct rambling aloe group to which our *A. tenuior* var. *viridifolia* belongs. All species are endemic to South Africa. Recognised as distinct, the Macrifoliae group was created in 1825 by the great English succulent student, Adrian Haworth. This was followed by others such as Berger (1908) and the doyen of aloes of Africa and Madagascar, Reynolds (1950). The generic name *Aloiampelos* is derived from the Greek *ampelos*, which means 'climbing', in reference to the climbing and scrambling nature of its seven species (Ellis 2013; Grace et al. 2013). Although *Aloe tenuior* was transferred to *Aloiampelos*, its four varieties were not, neither by Grace et al. (2013), nor by Ellis (2013). *Aloiampelos tenuior* is the most diverse species within the genus and the varieties named by Reynolds and the current author (var. *viridifolia*) are distinct and herewith transferred to *Aloiampelos*:

Aloiampelos tenuior var. *decidua* (Reynolds) Van Jaarsv., comb. nov.

Basionym: *Aloe tenuior* var. *decidua* Reynolds (*J. S. African Bot*. 2: 111, 1936). Type:—SOUTH AFRICA. Eastern Cape Province, Victoria East Div. (3226): Six miles north of Alice, (–DD), fl. 27 January 1936, *Reynolds 1760* (PRE, holotype; BOL, isotype).

PLATE 2363.—1, young branch, × 1; 2, inflorescence, × 1; 3, capsule, × 1; 4, opened capsules with seeds, × 1. Voucher specimen: *Van Jaarsveld, Voigt & Bayer 17832*, Compton Herbarium, Cape Town. Artist: Marieta Visagie.

Aloiampelos tenuior var. *densiflora* (Reynolds) Van Jaarsv., comb. nov.

Basionym: *Aloe tenuior* var. *densiflora* Reynolds (*The Aloes of South Africa*: 349, 1950). Type:—SOUTH AFRICA. Eastern Cape Province, 3326: Peddie Div., near Breakfast Vlei (25 miles south of Alice), (–BB), fl. 15 May 1937, *Reynolds 2390* (PRE, holotype).

Aloiampelos tenuior var. *rubriflora* (Reynolds) Van Jaarsv., comb. nov.

Basionym: *Aloe tenuior* var. *rubriflora* Reynolds (*J. S. African Bot*. 2: 108, 1936). Type:—SOUTH AFRICA. Eastern Cape Province, Pondoland, 3129: Steep slopes near the foot of Mlengana, 33 miles east of Umtata on road to Port St. Johns, (–CA), fl. 19 January 1936, *Reynolds 1750* (PRE, holotype).

The first unpublished revision of *Aloiampelos* was produced by Kristen Ellis in 2013 wherein she acknowledged seven species. *Aloiampelos* is at once distinguished from *Aloe* by its persistent resprouting rootstock and fast-growing, rod-like stems bearing distinct internodes with soft leaves. Most species grow in fynbos vegetation, which is subject to regular burning, hence the subterranean tuber and resprouting ability.

Along with *Aloiampelos tenuior*, the following six species of *Aloiampelos* are recognised (Botanical Database of Southern African Plants 2021): *A. ciliaris* (Haw.) Klopper & Gideon F.Sm., *A. commixta* (A.Berger) Klopper & Gideon F.Sm., *A. decumbens* (Reynolds) Klopper & Gideon F.Sm., *A. gracilis* (Haw.) Klopper & Gideon F.Sm., *A. juddii* (Van Jaarsv.) Klopper & Gideon F.Sm. and *A. striatula* (Haw.) Klopper & Gideon F.Sm. These species occur in fynbos, thicket, grassland or Afro-alpine vegetation. The best known species is probably the climbing aloe, *A. ciliaris*, the only true climber in subtropical thicket and savannas along the Eastern Cape coast that can reach heights of 10 m.

FIGURE 1.—*Aloiampelos tenuior* var. *rubriflora* with its showy red inflorescence. Photograph: E.J. van Jaarsveld.

Aloiampelos tenuior is a very variable and widespread species, and was first collected by James Bowie (about 1789–1869), horticulturist and botanical explorer under the British rule at the Cape. Bowie, as with many other staff members of the Royal Botanical Gardens, Kew, was sent to different parts of the world to collect plants of horticultural value and usefulness for the newly founded botanical garden. In 1816 he was instructed to sail to the Cape from Brazil by Joseph Banks, first director of the Royal Botanical Garden, Kew (Glen & Germishuizen 2010). On his third journey, Bowie ventured to Knysna (9 March 1820), further east via the Langkloof to Avontuur, then on to Uniondale, Uitenhage, Algoa Bay, Kowie, Grahamstown and finally back

TABLE 1.—Comparison of different varieties of *Aloiampelos tenuior* (adapted from Reynolds 1950)

Taxon	Distribution	Biome	Habit	Plant height	Leaf colour	Leaf margin	Perianth length and colour	Flowering time
A. tenuior var. *decidua*	Central, northern parts of Eastern Cape	Nama-Karoo	Erect shrublets	0.6 m	Glaucous green	Minutely denticulate, teeth 0.5 mm long	40 mm; peach-red	January, February
A. tenuior var. *densiflora*	Breakfast Vlei, near Peddie, central part of Eastern Cape	Albany Thicket	Erect shrublets, becoming scandent	0.45–0.70 m	Glaucous green	Minutely denticulate, teeth 0.5 mm long	25 mm; bright yellow, green-tipped	May
A. tenuior var. *rubriflora*	Kentani to Mzimvubu River, northeastern part of Eastern Cape	Coastal Grassland	Erect slender shrubs to 1.5 m tall, becoming scandent	Up to 0.26 m	Glaucous green	Minutely denticulate, teeth 0.5 mm long	20 mm; bright orange-red, green-tipped	January, February
A. tenuior var. *tenuior*	Gamtoos River and western part of Eastern Cape; KwaZulu-Natal	Albany Thicket	Rounded dense shrubs to 1 m tall with a tendency of becoming scandent	0.6–1.0 m	Glaucous green	Minutely denticulate, teeth 0.5 mm long	40–45 mm; dull scarlet, rarely yellow	October to January
A. tenuior var. *viridifolia*	Suurberg, in Addo Elephant National Park, Eastern Cape	Fynbos	Small rounded shrublet to 0.4 m tall	0.4 m	Glossy green	Entire	20 mm; yellowish-green	June, July

FIGURE 2.—*Aloiampelos tenuior* var. *decidua*, a non-scandent, erect shrublet growing in dry, inland habitat. Photograph: E.J. van Jaarsveld.

FIGURE 3.—Close-up of a flowering branch of *Aloiampelos tenuior* var. *densiflora*. Photograph: E.J. van Jaarsveld.

to Cape Town from Algoa Bay (29 January 1821) (Glen & Germishuizen 2010). It was on this journey that he encountered his three *Aloiampelos* species. The first was *A. gracilis*, a fynbos plant. Reaching the Gamtoos River and thicket vegetation, he gathered *A. ciliaris* and *A. tenuior* which are both locally abundant and common in the region. Typical *A. tenuior* grows in subtropical thicket or grassland and simply re-sprouts after occasional fires to which it is subjected. Bowie's three *Aloiampelos* species were named by Adrian Haworth in 1825.

A number of different varieties for *Aloiampelos tenuior* have been described (Reynolds 1950; Table 1). To place the subject of this contribution in context, we feature the different varieties of *A. tenuior* here, all of which grow widespread in the Eastern Cape. The variety *rubriflora* (Figure 1), a grassland and savanna species, occurs up

into northern KwaZulu-Natal. It has orange-red flowers and the plants are generally larger than those of the varieties *tenuior* and *decidua*. The variety *decidua* (Figure 2), a non-scandent, erect shrublet of up to 600 mm tall, flowers during midsummer and occurs in inland grassland regions, usually north of the Suurberg, from near Alice and Fort Beaufort to Bruintjies Hoogte in the dry Karoo in the north. This northern portion of its distribution range receives frost during the otherwise dry, cold winter and it has adapted to these climatic conditions by becoming deciduous. Furthermore, variety *decidua* is often subject to typical grassland fires, after which it simply resprouts. Variety *densiflora* (Figure 3) is similar to var. *tenuior*, but differs in that it has short, densely flowered inflorescences. Variety *tenuior*, perhaps the most attractive in the group, is mainly a plant from the subtropical thicket vegetation. The horticultural cultivar, *A. tenuior* var. *tenuior* 'Gamtoos' (Figure 4), is very floriferous and conspicuous during autumn when its yellow flowers appear.

FIGURE 4.—The floriferous cultivar *Aloiampelos tenuior* var. *tenuior* 'Gamtoos'. Photograph: E.J. van Jaarsveld.

Aloiampelos tenuior var. *viridifolia* (Figure 5) is the fifth addition to the *A. tenuior* complex and the only bearing glossy green leaves with an entire or almost entire margin. It occurs on the southern slopes at Kabouga in the Suurberg (Figure 6), and is the only variety recorded from dry fynbos (sclerophyllous Mediterranean-type vegetation). It is adapted to sun and semi-shaded situations.

FIGURE 5.—Close-up of a flowering branch of *Aloiampelos tenuior* var. *viridifolia*. Photograph: E.J. van Jaarsveld.

Aloiampelos tenuior var. *viridifolia*, then as *Aloe tenuior* var. *viridifolia* Van Jaarsv., was named in 2007 from a gathering on the eastern Suurberg in the Eastern Cape (Van Jaarsveld 2007). *Aloiampelos* has since been erected by Klopper and Smith (Grace et al. 2013) and, consequently, our species has been transferred to its rightful position within the genus *Aloiampelos*. What makes this variety distinct from the other four varieties of *A. tenuior* is its unique morphology

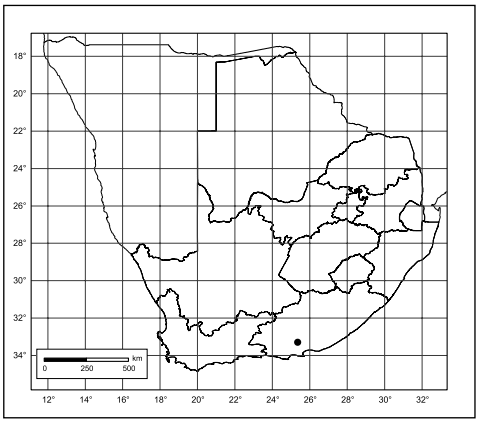

FIGURE 6.—Known geographical distribution of *Aloe tenuior* var. *viridifolia*.

and habitat. The type of var. *viridifolia* was gathered by Werner Voigt, Bruce Bayer and Ernst van Jaarsveld from Kabouga and grown at Kirstenbosch National Botanical Garden. The collected plant was immediately identified as belonging to the *Aloiampelos tenuior* species complex, however, the heads were smaller, consisting of soft unarmed leaves which were green (hence the specific epithet *viridifolia*), instead of glaucous as in other varieties of the species complex. Furthermore, the new variety flowered during the winter. When it flowered at Kirstenbosch, its affinity to *Aloiampelos tenuior* was confirmed and consequently named as a new variety. It was also the first time that *Aloiampelos tenuior* was collected in fynbos. The accompanying colour plate (Plate 2363) by Marieta Visagie was figured from the type collection kept at Kirstenbosch National Botanical Garden.

Koubouga is within the Addo Elephant National Park, which bodes well for our species' long term conservation future. *Aloiampelos tenuior* var. *viridifolia* plants are locally abundant, growing on steep southern and eastern slopes in typical fynbos vegetation. Plants are found at altitudes ranging from 300–500 m above sea level, in acidic quartzitic sandstone soil, which is low in mineral content. Plants occur scattered in and among rocks and can be difficult to detect when not in flower. Rainfall is throughout the year, but more frequent during summer and ranges from about 700–900 mm per annum. The vegetation in its habitat consists of Suurberg Quartzite Fynbos and *A. tenuior* var. *viridifolia* is frequently encountered with *Passerina* and *Agathosma* species and succulent plants such as *Haworthia cooperi* Baker and *Crassula cultrata* L. (Mucina & Rutherford 2006). Temperatures in its habitat are high during the day with an average summer daytime temperature of ± 26°C. The southern slopes are cooler with shady conditions and in winter very light frost may occur.

Adam Harrower, presently curating the succulent collection at Kirstenbosch since 2015, brought in a second collection of var. *viridifolia*, this time from the central Suurberg, near Ann's Villa, growing in the same dry fynbos vegetation. This supports our hypothesis that *Aloiampelos tenuior* var. *viridifolia* is a Suurberg fynbos endemic. Harrower also pointed out that the flowers are slightly scented, a unique feature for the genus. Considering the species' small, spreading, yellowish flowers, scent production is a good strategy for the plant to attract insects, in addition to sunbirds, for pollination.

Aloiampelos tenuior var. *viridifolia* grows readily and well in cultivation. It is easily propagated from either stem cuttings or grown from seeds. Cuttings will root rapidly in a sandy mixture during spring or summer. It also grows well in containers in a sandy, well-drained mixture. In regions where frost or snow is experienced during winter, it is best kept in a greenhouse, in fact, var. *viridifolia* is better adapted to shady greenhouse conditions compared to the other glaucous varieties. Plants should be pruned when they become untidy.

Other *Aloiampelos* species are cultivated throughout the world in warmer or Mediterranean-type climates. Plants are easily propagated from stem cuttings in situ and require little attention as they soon produce roots. Their persistent rootstocks make them tolerant to drought and, to some extent, frost. All can be grown in full sun, although *A. ciliaris* takes well to shade. *Aloiampels tenuior* var. *viridifolia* is best grown in fynbos gardens (Van Jaarsveld 2010). Other *Aloiampelos* species that are well-suited to fynbos gardens include *A. gracilis*, *A. decumbens*, *A. juddii* and *A. commixta*.

Key to the varieties of *Aloiampelos tenuior*:

1a: Plants small, erect, non-scandent shrublets; leaves glossy green or glaucous 2
1b: Plants erect shrublets becoming scandent; leaves glaucous. 3
2a: Leaves glossy green; racemes laxly flowered. . . . . .*A. tenuior* var. *viridifolia*
2b: Leaves glaucous; racemes densely flowered. . . . . *A. tenuior* var. *densiflora*
3a: Leaves becoming deciduous . . . . . .*A. tenuior* var. *decidua*
3b: Leaves evergreen 4
4a: Tall, slender shrubs; perianth orange-red . . . . . .*A. tenuior* var. *rubriflora*
4b: Erect, dense shrubs; perianth yellow . . . . . *A. tenuior* var. *tenuior*

Description.—Erect, branched shrubs, up to 0.4 m high, resprouting after fire. *Roots* slightly tuberous. *Branches* woody towards base, basally sheathing with internodes 8–10 mm apart; young branches fleshy with internodes 5–8 mm apart. *Leaves* soft, fleshy, ascending, in apical rosette of 80–140 mm in diameter; 25–70 × 18–28 mm, linear lanceolate, acuminate, dark glossy green, faintly striated, amplexicaul, decurrent on the stem and distinctly striated; adaxial surface flat to channelled, especially towards the stem, apex acute, mucronate; abaxial surface convex; margin entire; leaf sap clear. *Inflorescence* 1–3 simple, laxly flowered, erect racemes, up to 100–210 mm long; scape 50–90 mm long; bracts triangular-acuminate, grey-brown, lower bracts triangular, scarious, 4 × 5 mm, floral bracts smaller, 3–4 × 2 mm. *Flowers* spreading, becoming sub-pendent, buds green; perianth yellowish green, cylindrical-trigonous, 11–20 × 5 mm, outer segments free in upper half; filaments lemon yellow, sub-filiform; anthers exposed for 3–4 mm; pollen yellow; ovary cylindrical-globose, 3.5 × 2 mm, green; style 10 mm long, lengthening to 13 mm, protruding up to 6 mm. *Fruit* a capsule 11–13 × 5–6 mm, ascending spreading, with skeletal remains persisting for some time. *Seed* blackish grey, flattened, angular, 4 × 2 mm. *Flowering time*: in midwinter during June and July. Plate 2363.

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PLATE 2364 *Brunsvigia radulosa*

Brunsvigia radulosa Amaryllidaceae

Southern Africa

Brunsvigia radulosa *Herb*. in Flora Capensis: 280 (1837); Baker: 208–209 (1896); Dyer: 44–47 (1951); Pooley: 348 (1998); Pooley: 182 (2003); Zimudzi et al.: 114 (2008); Duncan et al.: 102 (2016); Manning: 62 (2019); Duncan et al.: 407 (2020). Brunsvigia burchelliana Herb.: t. 22 (1837). Brunsvigia cooperi Baker: 207 (1896).

The genus *Brunsvigia* Heist. is endemic to southern Africa, with its highest diversity in the Western Cape, Northern Cape and the midlands of KwaZulu-Natal (Snijman 2012). Currently, 18 species are recognised with five species having been illustrated in this journal, namely *B. undulata*, *B. josephinae*, *B. orientalis*, *B. elandsmontana* and *B. marginata* (Pole-Evans 1934; Dyer 1956, 1964; Killick 1977; Snijman & Smith 2001; Duncan et al. 2016). *Brunsvigia* is closely related to *Crossyne* and has similar morphological characters, such as raised, thick-walled margins, and bulbs with hard and bristly outer scales (Snijman & Linder 1996). The latter character is also shared with two other genera, *Ammocharis* and *Cybistetes* (now also incorporated in *Ammocharis*) (Snijman & Linder 1996). A phylogenetic study of the mainly African tribe, Amaryllideae, by Snijman & Linder (1996) using morphological, seed anatomical and cytological data resulted in a monophyletic clade of *Brunsvigia* and *Crossyne*.

The genus name was first published in 1755 by Lorenz Heister (1683–1758) in honour of Karl Wilhelm Ferdinand, Duke of Brunswick-Lüneburg and Prince of Brunswick-Wolfenbüttel (Snijman 2005; Duncan et al. 2016). *Brunsvigia* is characterised by bulbs that are usually large, either subterranean or partly above ground. Its leaves are distichous at the base of the stem, prostrate, outspread, suberect or erect; narrowly to broadly tongue-shaped, oblong or ovate; adaxial surfaces are glabrous, smooth to papillate; abaxial surfaces also glabrous; margins are thick textured, crispulate and reddish (Dyer 1950; Manning et al. 2002; Snijman 2005; Zimudzi et al. 2008; Duncan et al. 2016). Inflorescences attract a diverse range of pollinators, from Noctuid moths to sunbirds (Manning et al. 2002; Snijman 2005).

The fleshy seeds are dispersed through wind-tumbling (in their natural habitat) whereby ripe peduncles detach at ground level and the infructescence tumbles away in the wind, scattering seeds along the ground (Duncan et al. 2016). The dispersal of seeds coincides with seasonal changes, either during late autumn and winter (for species in winter-rainfall areas) or summer and early autumn (for species in summer-rainfall areas) (Duncan et al. 2016).

Brunsvigia radulosa bears up to 75 individual pinkish flowers on a thick peduncle in a subglobose umbel. According to Ward & Johnson (2005) the flowers are predominantly pollinated by a species of long-proboscid horse fly (*Philoliche aethiopica*) although, in areas where the horse fly's habitat have been destroyed, bees act as pollinators. The leaves of

PLATE 2364.—Flowering plant in habitat, × 0.5. Voucher specimen: *Archer 2557*, National Herbarium, Pretoria. Artist: Gillian Condy.

B. radulosa are prostrate, rarely suberect, tongue-shaped or oblong, dark green and with translucent (rarely reddish) margins. The flowers tend to be denser, rarely widely spreading (Duncan et al. 2016).

Brunsvigia radulosa closely resembles *B. natalensis*, but differs in a number of characters, such as flowering time, leaf shape and orientation, and peduncle and pedicel dimensions (Table 1). It is worth noting that Baker (1896) in *Flora Capensis* did not list any characters to differentiate *B. radulosa* from *B. natalensis* other than to indicate that *B. radulosa* is 'imperfectly known'. It is possible that Baker relied on type material, of which *B. radulosa* is an incomplete specimen consisting only of a leaf, and thus could not differentiate between the two species. Dyer (1951) continued using the name *B. radulosa*, after it was adopted by Baker in 1896, instead of *B. burchelliana*, acknowledging the difficulties in separating and identifying with confidence other plants with the original type material of *B. radulosa* as the only reference. However, he indicated that only one species is recognised from the place where the type specimen was collected by the English explorer William Burchell in 1813, near Hondeblafs River, Philipstown, in the eastern Northern Cape (Herbert 1837; Dyer 1951; Duncan et al. 2016). Baker also identified specimens collected from the same area by Cooper as *B. radulosa*, only for him to later rename them as *B. cooperi* (Dyer 1951). According to Dyer (1951), the renaming of the Cooper specimens was incorrect, as they consisted only of floral parts. Furthermore, the description of *B. cooperi* was based on the identity of a specimen that Dyer (1951) found debatable (Baker 1896; Kew 2021). This would have allowed Dyer (1950, 1951) to have a full picture of *B. radulosa*, hence he was able to raise his concern about the resemblance between *B. radulosa* and *B. natalensis*, citing difficulties in differentiating them when reviewing the genus. Referring to other material Dyer examined for the revised description of the species, he emphasised in *Plant Life* (1951) that, 'I have gone further and have included plants from Bechuanaland, Transvaal and Natal'. Archer & Archer (2005) concurred with Dyer's (1951) observations and emphasised the need for additional data on morphological variation over the entire range of the species in order to reassess its taxonomic limits. Duncan et al. (2016) also noted and acknowledged the observations made by Dyer (1950) regarding the two species. Therefore, the circumscriptions of the two species, as accepted by Dyer (1950, 1951), are followed here.

In 1837, Herbert provided a short description of *Brunsvigia radulosa* and also a plate of *B. burchelliana* relying on the same type specimen of the leaf collected by Burchell for both the description and a plate (Herbert 1837; Global Plants Jstor 2020). Only a description of *B. radulosa* was provided from the leaf specimen (Herbert 1837), although both

TABLE 1.—Differences between *Brunsvigia radulosa* and *B. natalensis* by different authors

Author	*B. natalensis*	*B. radulosa*
Dyer (1950)	Peduncle to 250 mm high; pedicels to 120 mm long; flowering from November to early December.	Peduncle to 500 mm high; pedicels to 300 mm long; flowering mostly from February to March.
Duncan (2016)	Leaves narrower, spreading to suberect; heads fewer-flowered with tepals more widely spreading; flowering in October.	Leaves broader and more prostrate; flowerheads denser; flowering in late January.

species were published in the same publication. Herbert noted the error and in the text accompanying the plates, he noted, '*Brunsvigia Burchelliana*, leaf. Herb. Burchell. see. *B. radulosa* p. 281, to be corrected *Burchelliana*, for I believe I have the plant, and the green leaf is not rasped as it appears when dry' (Herbert 1837). Therefore, *B. radulosa* would have had to be synonymised under *B. burchelliana* (Herbert 1837), however, Baker (1896) opted to use the name *B. radulosa*.

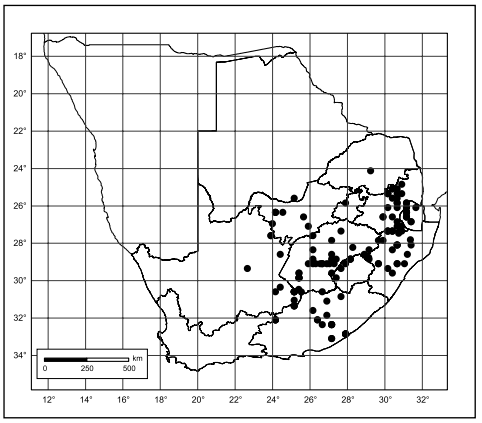

FIGURE 1.—Known distribution of *Brunsvigia radulosa* in southern Africa based on data from the National Herbarium, Pretoria (PRE) and iNaturalist (2021).

Brunsvigia radulosa has a wide distribution range in southern Africa, from south-eastern Botswana to Limpopo, Mpumalanga, Gauteng, North West, Free State, KwaZulu-Natal, Eastern Cape and the eastern part of the Northern Cape in South Africa (Duncan et al. 2016). The species has also been recorded in Lesotho and Eswatini, as shown in Figure 1 (Duncan et al. 2016; Plants of Southern Africa 2020; iNaturalist 2021), and it occurs in marshy grassland areas and swamps as single individuals (Figure 2), or in small or large colonies (Duncan et al. 2016). Flowers appear in summer, from January to February. There is an inconsistency between the appearance of leaves and flowers: usually the leaves are produced before flowerheads, but it can be the other way around, depending on where the species is growing (Duncan et al. 2016).

In the Eastern Cape Province of South Africa *Brunsvigia radulosa* is sympatric with *B. gregaria*. The two species can readily be distinguished due to their different heights. *Brunsvigia radulosa* is taller (flowering specimens up to 800 mm high) than *B. gregaria* (flowering specimens up to 400 mm high). In its KwaZulu-Natal distribution range, the pinkish flower colour of *B. radulosa* is often confused with flowers of *B. grandiflora*. The two species differ in that *B. radulosa* has prostrate, rarely suberect, broadly elliptic leaves, compared to the erect to suberect, broadly linear leaves of *B. grandiflora*.

The presence of antineoplastic anhydrolycorinium chloride in *Brunsvigia radulosa* is thought to relate to its ethnomedicinal application in the treatment of abdominal pain (Crouch et al. 2002). *Brunsvigia radulosa* is one of the plants used in the Kamberg region of KwaZulu-Natal in the preparation of herbal concoctions where bulb material is chopped and dried before being placed in cold water that is then boiled (Crouch et al. 2002). The chemical components of the bulb of *B. radulosa* include at least 12 iso-quinoline alkaloids (Crouch et al. 2002). The leaves of the species are reportedly used to wash divining bones by traditional healers to ensure accurate diagnosis (Sobiecki 2008).

Brunsvigia radulosa and *B. natalensis* are cultivated in the same way and are well suited to grow in containers with a diameter of 300–350 mm. They require full sun and a well-drained medium containing balanced inorganic matter, such as coarse river sand, and composted

FIGURE 2.—*Brunsvigia radulosa* in its natural habitat. Photograph: R.H. Archer.

bark. A substantial amount of watering (once a week to every 10 days in summer) is also needed (Duncan et al. 2016). Seedlings need special attention during their early developmental stages to avoid wilting due to either lack of adequate moisture or over-watering (Archer & Archer 2005).

The species epithet refers to the roughness of the upper leaf surface (Duncan et al. 2016). Common names include candelabra flower; *kandelaarblom*, *misryblom* (Afrikaans); *lemathla* (Southern Sotho) (Archer & Archer 2005).

The species is not threatened (Snijman & Victor 2004).

Description (after Duncan et al. 2016).—Deciduous, summer-growing, up to 800 mm high when in flower. *Bulb* solitary, subterranean, ovoid, 65–200 mm in diameter; neck 50–100 mm long; outer tunics hard, dark brown. *Leaves* 4 to 6, prostrate, rarely suberect, broadly elliptic, 250–500 × 100–200 mm, leathery, often appearing with flowers, on other occasions appearing afterwards; adaxial surface flat, dark green, unmarked, rough-textured; margins flat, colourless (rarely reddish), rough-textured. *Inflorescence* a hemispherical umbel, 30- to 75-flowered, 480–720 mm in diameter; peduncle erect, 300–500 mm long, 25–35 mm in diameter, bright green, glabrous, striate; spathe bracts 2, ovate-lanceolate or ovate, 60–80 × 25–50 mm, translucent green with darker veins, thin-textured; pedicels radiating, 170–300 mm long, light to dark green, occasionally shading to reddish-brown apically. *Flowers* spreading, zygomorphic, ± widely funnel-shaped; deep red, bright pink, pinkish-red or pink; perianth tube funnel-shaped, 2.5–5.0 mm long; tepals oblong-lanceolate, 38–55 × 8–12 mm, acute, 3 upper tepals ± ascending, 2 lateral tepals spreading, lower tepal decurved, margins flat or slightly undulate. *Stamens* shortly exserted; filaments 40–50 mm long, pink or red; anthers oblong, 10–12 mm long; pollen cream. *Ovary* 3-angled, 15–40 mm long, brownish-red or pink; style declinate, rarely exserted beyond anthers, 47–56 mm long, pink or red; stigma minutely 3-branched. *Capsules* ± obconical, broadly 3-angled, 15–40 mm long, light brown and papery when ripe. *Seeds* ± globose, 5–6 mm in diameter, light green. *Flowering time*: January–February. Plate 2364.

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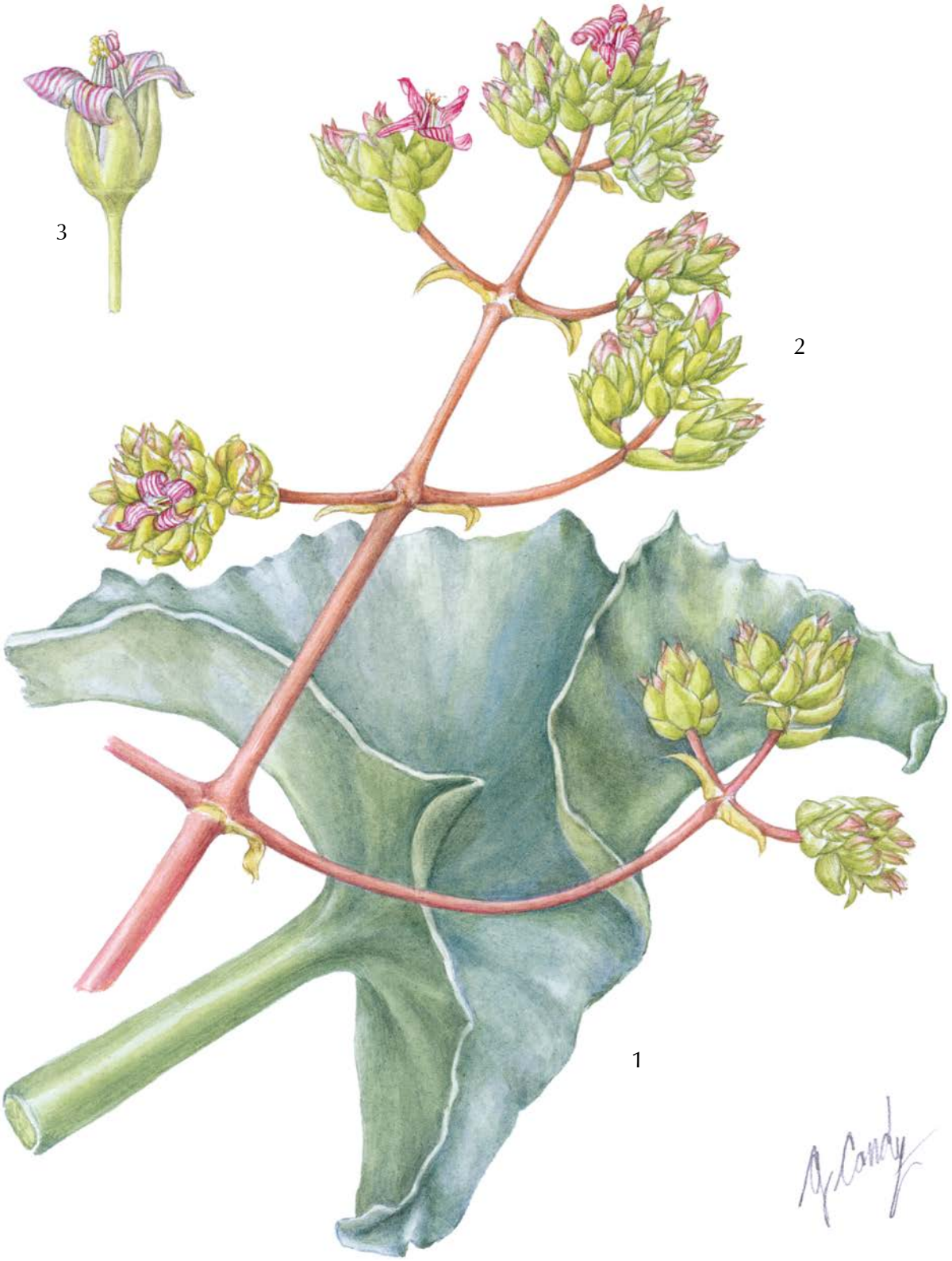

PLATE 2365 *Kalanchoe beharensis*

Kalanchoe beharensis Crassulaceae: Kalanchooideae

Madagascar

Kalanchoe beharensis *Drake* in Bull. Mus. Histoire Natural (Paris) 9: 41 (1903). Hamet: 29 (1908); Fournier: 76, Plate 76 (1935); François: 33, Plate XVI (1937); Jacobsen: 641, 642, Figures 847, 848 (1960); Raymond-Hamet & Marnier-Lapostolle: 33, Plate IX, Figures 20–22, Plate X, Figure 23 (1964); Hargreaves & Hargreaves: 7 (1972); Jacobsen: 283, Plate 103, Figure 2 (1974); Allorge-Boiteau: 9, 11, 14, 16, Photo 8 (1995); Boiteau & Allorge-Boiteau: 154–156, 158 (1995); Rauh: 116 (1995); Rauh: 300–302, Figures 1095–1109 (1998); Descoings: 147 (2003); Walters et al.: 257 (2011); Smith et al.: 307 (2017); Smith et al.: 244 (2019b). *Kalanchoe vantieghemii* Raym.-Hamet in J. Bot. (Morot) 20: 109 (1906), as '*van Tieghemi*'.

Up to his death, Raymond-Hamet (25 March 1890 [Dijon, Côte D'Or, France]–2 October 1972 [Paris, France]) was regarded as the undisputed international expert on the genus *Kalanchoe* Adans. (Crassulaceae subfam. Kalanchooideae) (Smith 2020a). He described his first species of *Kalanchoe* at the age of 16 and by the time he was 20 had already published a comprehensive, multi-part revision of the genus. The first name that Raymond-Hamet published in *Kalanchoe* (Hamet 1906) was *K. vantieghemii* Raym.-Hamet, as '*van Tieghemi*', but it turned out to be a nomenclaturally superfluous name, as it was a redescription of the subject of this paper. Three years earlier, based on material collected by Guillaume Grandidier (1873–1957) in Madagascar, Drake del Castillo (1903) had published the name *K. beharensis* Drake. Note that around 1912/1913 Raymond Hamet changed his name to 'Raymond-Hamet', or at least started writing his name in this way when authoring papers. In this paper his publications are cited under either 'Hamet, R.', or 'Raymond-Hamet', depending on which version of his name he used in the publication referenced. The abbreviation of Raymond-Hamet (and Raymond Hamet, for that matter) as an author of plant names is 'Raym.-Hamet' (Brummitt & Powell 1992: 255, 524).

Kalanchoe beharensis is one of the largest members of the genus and, reaching a height of about 3 m, one of only a few kalanchoes that can truly be regarded as arborescent (Smith et al. 2019a) (Figure 1). The species carries its flowers erect or spreading (not pendulous), has rather woody stems and branches, leaves that are not bulbiferous, and, as presently widely treated, belongs in *Kalanchoe* subg. *Kalanchoe* (Smith et al. 2019b). Boiteau & Allorge-Boiteau (1995) placed *K. beharensis* in their informal Groupe X: Lanigerae (Smith et al. 2019b). This group of 14 species includes the largest-growing plants of the genus. However, it includes taxa with different types of flowers, along with transitional species. One of the two subgroups includes species with a distinctly urceolate corolla with reduced segments and a highly reduced calyx, often with strongly fleshy sepals. The plants are glabrous or with sagittate or stellate hairs. Of the arborescent *Kalanchoe* species, *K. arborescens* and *K. grandidieri* are included here. The second subgroup is characterised by a corolla with more developed lobes, never urceolate, and a more developed calyx. The hairs are trifurcate. This subgroup includes *K. beharensis* and its apparently closest relative,

PLATE 2365.—1, leaf, × 0.3; 2, inflorescence, × 0.5; 3, flower, × 2. Voucher specimen: *G.F. Smith 1077* in H.G.W.J. Schweickerdt Herbarium, Pretoria. Artist: Gillian Condy.

FIGURE 1.—*Kalanchoe beharensis* grows as small to medium-sized, erect to leaning, trees that can reach a height of 3 m. The form of *K. beharensis* most often encountered in South Africa has large, light bluish grey, velvety, boat-shaped leaves. Photograph: G.F. Smith.

K. dinklagei (syn. *K. brevisepala* L.Allorge, the name used in Boiteau & Allorge-Boiteau 1995: 158) (see Smith et al. 2019a). Among other characters, *K. beharensis* is distinguished by having lateral inflorescences as opposed to the terminal ones of *K. dinklagei*.

Although *Kalanchoe beharensis* is a very variable species with numerous forms, having been variously treated as worthy of recognition as cultivars, none of these forms have been formally described at infraspecific ranks. Shaw (2008) provided a checklist of *Kalanchoe* cultivars in which an impressive 625 were tabulated, the majority named with their parental species, together with the name of the originator if known, references, and additional notes. For *K. beharensis* 17 named entities were included. Two designations that have never been validly published are sometimes encountered for material in cultivation: *K. beharensis* 'var. aureo-aeneus' H.Jacobsen, treated by Shaw (2008) as 'Aureo-aeneus', has leaves that are ad- and

FIGURE 2.—The form of *Kalanchoe beharensis* variously known as 'var. subnuda' ('Subnuda') or 'var. aureo-aeneus' ('Aureo-aeneus') has leaves that are adaxially virtually glabrous. Photograph taken on 12 April 2017 in the Jardin Majorelle in Marrakech, Morocco. Photograph: E. Figueiredo.

abaxially densely covered in short, golden brown hairs. In contrast, the leaves of *K. beharensis* 'var. subnuda' H.Jacobsen, treated by Shaw (2008) as 'Subnuda', are variously sparsely covered in hairs on the abaxial side, and virtually glabrous adaxially (Figure 2). An interesting form of which especially the abaxial leaf surfaces are adorned with short but prominent, stalactite-like warts is known as cultivar 'Fang', but this is an interspecific hybrid *K.* ×*edwardii* Gideon F.Sm. & Shtein, of which *K. beharensis* is one parent (Figure 3) (Smith & Shtein 2020).

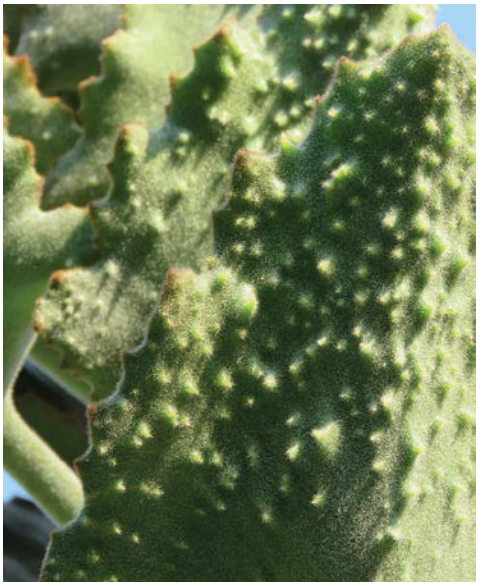

FIGURE 3.—Both the ab- and adaxial surfaces of the leaves of *Kalanchoe* ×*edwardii* 'Fang' are adorned with prominent protuberances. Photograph: G.F. Smith.

The form that is encountered in cultivation in southern Africa is remarkably uniform in the expression of its characters: it has large, light green to glaucous leaves of which both surfaces are velvety and the basal 'wings' of the leaf blade stretch well past the point of attachment of the petiole

FIGURE 4.—The form of *Kalanchoe beharensis* widely cultivated in southern Africa has large, light green to glaucous leaves. The basal 'wings' of the leaf blade stretch well past the point of attachment of the petiole to the blade. Photograph: G.F. Smith.

FIGURE 5.—The scars left where the leaves were shed lower down on the stems and branches of *Kalanchoe beharensis* are conspicuously edged with sharp points. Photograph: G.F. Smith.

to the blade (Figure 4). Because of the distinctive shape, size and texture of the leaves of the species, common names recorded for it locally include *donkie-oor* and *fluweelblaar* in Afrikaans, and donkey's ear, elephant's ear (kalanchoe) and velvet leaf (kalanchoe) in English. Unlike several of the other, weaker forms of *Kalanchoe beharensis*, the one common in southern Africa grows very strongly and has become naturalised in a few places in the mild-climate eastern parts of the subcontinent (Smith et al. 2019b). The bark of *K. beharensis* is resinous (Jadin & Juillet 1912) and the stems, with their prominent 'spikes' left where leaves abscised, also lend interest to plants in cultivation (Figure 5).

Kalanchoe beharensis has also been used as one parent – the other parent is *K. millotii* Raym.-Hamet & H.Perrier – in the nothospecies *K.* ×*hummeliae* Gideon F.Sm.

FIGURE 6.—*Kalanchoe beharensis* and *K. millotii* are the parents of the nothospecies *K.* ×*hummeliae*, pictured here. Photograph: G.F. Smith.

(Smith & Figueiredo 2019; Smith 2020b). *Kalanchoe* ×*hummeliae* is in all respects a smaller plant than the form of *K. beharensis* found in gardens in southern Africa, with the general growth form, leaves, and flowers intermediate between those of its two parents (Figure 6). *Kalanchoe millotii* is also a parent of the recently described *K.* ×*gildenhuysii* (Smith & Figueiredo 2020).

FIGURE 7.—*Kalanchoe beharensis* can be easily propagated from single leaves with intact petioles. Plantlets rapidly develop on the cut end of a petiole once the wound has sealed. The leaf blade slowly becomes desiccated as the plantlets develop. Photograph: G.F. Smith.

Kalanchoe beharensis flowers from June to September (southern hemisphere), with a peak in July. The species is self-fertile and plants produce copious amounts of very fine, dust-like seeds that germinate very easily. The production of seed in significant volumes, the viability of the seed, and ability of new plants to grow from abscised leaves (Figure 7) or even from damaged leaves still attached to the plant, have contributed to *K. beharensis* having become established in southern Africa. The facility of *K. beharensis* to colonise new habitats even led Raymond-Hamet (1941) to speculate and conclude that the recorded presence of the species in Tanzania in East Africa as early as August 1910 was because it occurred there

FIGURE 8.—Portion of an inflorescence of *Kalanchoe beharensis*. All the parts are finely tomentose. The recurved corolla lobes are distinctly purple-striped. Photograph: G.F. Smith.

FIGURE 9.—A cluster of flowers of *Kalanchoe beharensis*. In the bud stage the corolla are virtually entirely obscured by the sepals. Photograph: G.F. Smith.

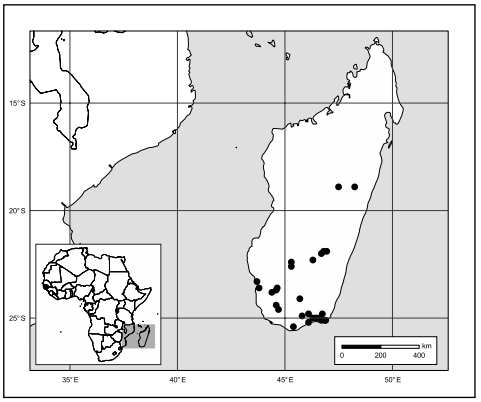

FIGURE 10.—Geographical distribution range of *Kalanchoe beharensis* in Madagascar based on information held in the Global Biodiversity Information Facility, specimens cited in Boiteau & Allorge-Boiteau (1995: 158) that was used for Map 17 [p. 202, page not numbered] reproduced in that work, and other exsiccata. See text for a discussion.

naturally. Raymond-Hamet could not otherwise explain how material had reached the vicinity of the Imperial Biological-Agricultural Experimental Station at Amani near the Usambaras – an escape from cultivation at Amani was not a possibility for him. As happens very often, exotic species, including *K. beharensis*, were introduced to the garden of the Amani Station and many spread into and became established in natural vegetation (Conte 2004).

Kalanchoe beharensis is exceedingly easy and very popular in general cultivation as it is very drought-hardy and the furry leaves and spiky stems and branches lend interest and texture to a garden. In addition, during the drab winter months, huge, laterally-borne inflorescences (Figure 8) bear large numbers of flowers with reddish purple-striped petal lobes (Figure 9). Plants grow in virtually any soil type, and require very little aftercare. However, *K. beharensis* is not frost-hardy and the leaves and growing tips of the branches can be severely damaged during a cold spell, even if it is not accompanied by frost. Propagation is through seed, stem truncheons, or branch cuttings. Severed leaves with the petiole intact will also easily strike root. Be sure to place the leaves on top of (not in) the soil; plantlets and roots will soon form.

Kalanchoe beharensis occurs naturally in the western, central, and eastern parts of southern Madagascar, including at Behara, for which the species is named (Boiteau & Allorge-Boiteau 1995: p. 202 [page not numbered], Map 17; Rauh 1995: 116; Allorge-Boiteau 1996: 144, Map 18) (Figure 10). From an investigation of exsiccata available in various herbaria, it is likely that the species has become established in Madagascar beyond its natural distribution range in the south of the island. *Kalanchoe beharensis* has been introduced to several mild-climate parts of the world and is now widespread in cultivation.

All three photosynthetic pathways, C3, C4, as well as crassulacean acid metabolism (CAM) have been recorded in species of *Kalanchoe*. Species of this genus, notably

K. daigremontiana, *K. fedtschenkoi* and *K. tubiflora*, have been used as model taxa in unravelling the mechanism and ecological significance of CAM (Smith et al. 2019b). However, the first comprehensive field study, in Madagascar, of CAM involved the use of *K. beharensis* (Kluge et al. 1992). The study showed that this species is capable of maintaining full CAM performance throughout an entire arid season, thus avoiding CAM idling. It was assumed that this capability was based on maintenance of appropriate water status in the photosynthetically active leaves even during long-lasting drought. This capability was found to be due to minimisation of cuticular transpiration by the extreme CAM mode accompanied by water transfer from the older leaves which then wilt and are shed.

Description.—Perennial shrubs or small trees, sparsely branched, with haphazardly rounded canopies, robust succulent, to 3 m tall. *Stem* simple lower down, branched from ± 1 m above the ground, thick, to 150 mm in diameter, ± straight or variously curved, surface prominently covered by sharp projections left by expanding, prominent leaf scars; bark light brownish grey, flaking, flimsy. *Leaves* few to many towards terminal half of branches, shed lower down to yield leaf scars, erect to variously curved, succulent, densely pubescent, petiolate, ± flattened above and below, dull yellowish green to glaucous; petiole 40–100 mm long, same colour as leaf blade, succulent; blade 60–450 × 70–350 mm, somewhat elongated-triangular, deltoid to peltate, irregularly folded lengthwise and in width, succulent; base flared downwards beyond point of attachment of petiole, rarely somewhat cuneate; apex rounded-obtuse or truncate; margins irregularly toothed. *Inflorescence* an axillary, densely branched, many-flowered panicle, up to 800 mm long, rounded, erect to gracefully curved sideways and upwards; pedicels 5–12 mm long, densely pubescent. *Flowers* ± erect or slanted in various directions, densely pubescent, subtended by prominent bracts that are soon shed, creamy to greenish pink to pale yellow to yellowish green with longitudinal reddish purple stripes prominent on corolla lobes, less so on corolla tube; calyx light greenish white, very lightly infused with purple, especially towards tip, with or without feint longitudinal reddish purple stripes; sepals 5–7 mm long, elongated-triangular, fused below for ± 2 mm, acute, obscuring the corolla tube; corolla tube 6–7 mm long, more or less quadrangular-urceolate, tapering to the mouth, 4-angled; corolla lobes 3 × 4 mm, deltoid, strongly recurved, apiculate. *Stamens* inserted in the middle of the corolla tube or higher up, exserted for 1–2 mm; filaments ± 5 mm long, thin, light greenish white; anthers ± 0.5–1.0 mm long, yellow, exserted. *Pistil* consisting of 4 carpels; carpels 3–4 mm long, light yellowish green; styles 7–9 mm long; stigmas light brownish yellow, very slightly capitate; scales ± 3 × 1 mm, rectangular, connate, truncate above, slightly apiculate. *Follicles* 6–7 mm long, dark brownish black, brittle, grass spikelet-like when dry, enveloped in dry, greyish black remains of corolla. *Seeds* 0.75–1.00 mm long, dark brown to black, rectangular to slightly banana-shape-curved, tapering to both ends. *Chromosome number*: $n = 18$ (Baldwin 1938; Friedmann 1971; Rabakonandrianina & Carr 1987). Plate 2365.

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Kalanchoe crouchii Crassulaceae: Kalanchooideae

South Africa

Kalanchoe crouchii *Gideon F.Sm. & Figueiredo* in Haseltonia 25: 87 (2018).

The family Crassulaceae, which includes between 34 and 45 genera depending on which taxonomic concept is followed, has a very wide global distribution range in which areas of high present-day species diversity can be readily delimited. These include the southern African subcontinent, Mexico and abutting southwestern North America, Mediterranean Europe, and parts of Asia (Thiede & Eggli 2007). In southern Africa five crassuloid genera occur naturally: *Adromischus* Lem., *Cotyledon* L., *Crassula* L., *Kalanchoe* Adans. and *Tylecodon* Toelken (Tölken 1985). With the exception of *Crassula*, the other four genera are all included in Crassulaceae subfam. Kalanchooideae. Collectively, the five crassuloid genera are represented by about 250 species in the subcontinent; to this number *Kalanchoe* contributes 20 species (Smith et al. 2019; Smith & Figueiredo 2021). Globally though, with ca. 200 species, *Kalanchoe* is the third largest genus recognised in the Crassulaceae (Descoings 2003). Four subgenera, *K.* subg. *Kalanchoe*, *K.* subg. *Bryophyllum* (Salisb.) Koord., *K.* subg. *Kitchingia* (Baker) Gideon F.Sm. & Figueiredo and *K.* subg. *Fernandesiae* Gideon F.Sm., are recognised in *Kalanchoe* (Smith & Figueiredo 2018a); with the exception of the round to somewhat soup plate-leaved species all of which fit in *K.* subg. *Fernandesiae*, the balance of the southern African species are included in the autonymic subgenus.

Three of the 20 southern African species of *Kalanchoe* Adans., *K. longiflora* Schltr. ex J.M.Wood (Smith & Figueiredo 2017), *K. luciae* Raym.-Hamet (Smith et al. 2019) and *K. sexangularis* N.E.Br. (Figueiredo et al. 2016), have become enormously popular in domestic and amenity horticulture in South Africa. Both *K. longiflora* and *K. sexangularis* serve as very useful, waterwise groundcovers, especially when they are in the vegetative phase. When planted en masse their turquoise-green and bright red leaves, respectively, produce truly eye-catching displays. Their erect to leaning, rather diffuse inflorescences carry apical clusters of bright yellow, erectly-borne flowers that eventually tower and topple over the fairly low-growing pseudo-rosettes. The third species, *K. luciae*, with its red- to purple-infused, soup plate-sized leaves, is an excellent accent plant that will grow vegetatively for two to three years, before producing, under optimal growing conditions, a very large, densely flowered, club-shaped inflorescence that can reach a height of well over 1 m. Of these three species, only *K. sexangularis* has thus far been featured in the pages of *Flowering Plants of Africa* (Tölken 1983).

Until recently, only two species of southern African *Kalanchoe* with large, obovate to round leaves were widely upheld: *K. thyrsiflora* Harv., which holds the distinction of having been the second *Kalanchoe* species to be described from South Africa (Harvey 1862) and the

PLATE 2366.—1, non-flowering plants on dolomitic shelf, × 0.1; 2, inflorescence, × 1.3; 3, half flower, × 5; 4, pistil with squamae, × 6; 5, open follicles, × 2. Voucher specimen: *N.R. Crouch 1297* in Buffelskloof Herbarium, Lydenburg [Mashishing]. Artist: Angela Beaumont.

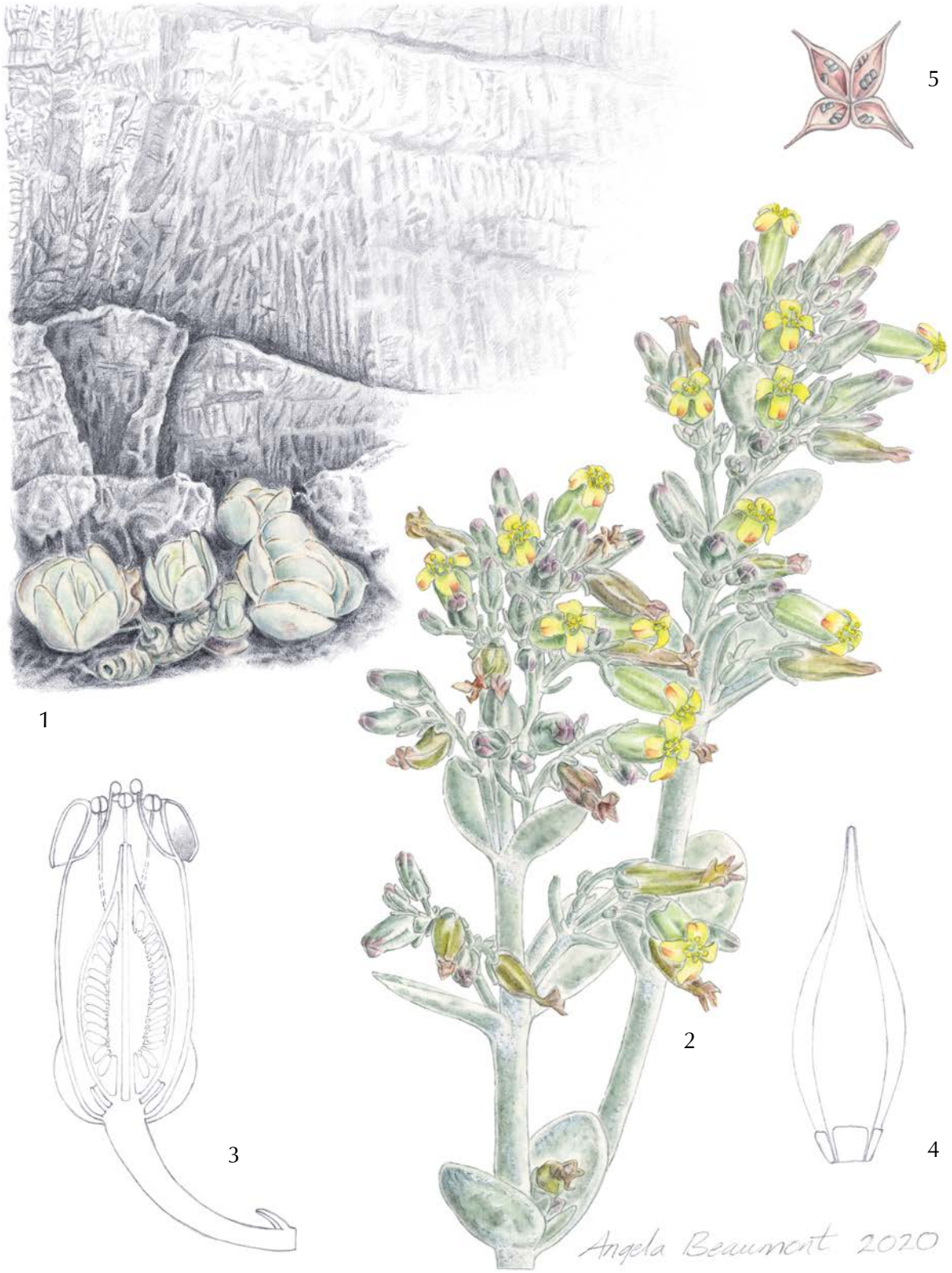

PLATE 2366 *Kalanchoe crouchii*

first kalanchoe to have been illustrated in *The Flowering Plants of South Africa* (Phillips 1929), as this journal was then known, and *K. luciae*. In *K. luciae* two subspecies were recognised: the autonymic one and *K. luciae* subsp. *montana* (Compton) Toelken. However, since 2016, two new species, *K. winteri* Gideon F.Sm., N.R.Crouch & Mich.Walters (Crouch et al. 2016) and *K. crouchii* Gideon F.Sm. & Figueiredo (Smith & Figueiredo 2018b) were described in the group in short order, and *K. montana* Compton was reinstated to species rank (Smith et al. 2016). One of these species, *K. crouchii*, is the subject of this paper (Figure 1).

Kalanchoe crouchii was first collected a little over a century ago in September 1919 by the indefatigable amateur botanist, Archdeacon Frederick A. Rogers, the gatherer of the types of many names of South African plants, and for whom several species were named, including *Sterculia rogersii* N.E.Br. and *Anisotes rogersii* S.Moore. His material (*F.A. Rogers s.n. sub PRE 53520*) from near Pilgrim's Rest made its way via the National Herbarium (PRE) to the Crassulaceae taxonomist, Selmar Schonland, at the Albany Museum in Grahamstown. In his report back to the National Herbarium, Schonland indicated that he considered the material to be '…quite different from *K. thyrsiflora*' and expressed his desire to see more specimens from the Pilgrim's Rest locality; these seemingly were never provided. Decades later, L.E.W. Codd collected and grew on a plant from the same general locality (Pilgrim's Rest), and in 1959 had photographs taken of flowering material. The resultant black and white prints are filed in PRE, and on their back is a reference to *Codd*

FIGURE 1.—*Kalanchoe crouchii* plants are solitary or with up to five rosettes, sparsely branched from near the base. Leaf margins are smooth, the same colour as the blade, or bronze. Photograph: N.R. Crouch.

FIGURE 2.—The flowers of *Kalanchoe crouchii* are only 10–11 mm long, erect to slanted horizontally. The tepal lobes bear a whitish waxy bloom below but above are bright yellow and tipped on one side with an apical flush of brick red. Photograph: N.R. Crouch.

9798 (seemingly accessioned as PRE0390356-0), which has so far not been found by us in that repository. Further details on this historical matter are provided by Smith & Figueiredo (2018b). Codd's record has long confounded botanists: it had caught the attention of Compton (1967) who, in his protologue for *K. montana* Compton, thought that it appeared to be conspecific with his new species. However, Smith et al. (2016) considered the photograph a better match for *K. winteri* than *K. montana*. Field work was clearly required, and so, informed by the precise locality data associated with Codd's collection, a visit was made by one of us (NRC) to the site in the early summers of 2016 and 2017, when the species was relocated and confirmed to be new.

Kalanchoe crouchii differs from *K. luciae* in consistently having golden yellow instead of whitish, pale yellowish green, or pale pink corolla lobes, and narrowly urceolate rather than ellipsoid corolla tubes (Figure 2). *Kalanchoe crouchii* differs from *K. winteri* in its leaves not being basally auriculate. It differs from *K. thyrsiflora* in having narrowly urceolate corolla tubes instead of cylindrical ones, corolla tubes that are significantly shorter (9–10 mm relative to 12–20 mm long), filaments inserted higher in the corolla tube, and all eight anthers exserted rather than just four. *Kalanchoe crouchii* differs from *K. montana* by being completely glabrous rather than most often tomentose. *Kalanchoe crouchii* differs from all these species by being smaller in all respects, with glaucous leaf blades that are usually bronze-infused along

the margins, rather than frequently deep pink- to bright red-infused throughout. *Kalanchoe crouchii* has the narrowest, most nearly cylindrical ovaries of all of them, a feature illustrated by Smith & Figueiredo (2018b: Figure 13). Once dry, the reddish brown follicles of *K. crouchii* (Figure 3) split star-shaped to release the very fine, dust-like seed.

Kalanchoe crouchii is endemic to South Africa's Mpumalanga Province where it has so far only been collected in the vicinity of the historic gold mining town of Pilgrim's Rest (Figure 4). The plants occur in grassland on northern aspects where they obtain protection from fire by growing in shallow humic-rich pockets along the ledges of dolomite boulders (Figure 5). The species occurs at an altitude of ca. 1 400 m above sea level, in Northern Escarpment Dolomite Grassland (Gm 22) (Mucina et al. 2006) within the Wolkberg Centre of Endemism (Van Wyk & Smith 2001). Other Crassulaceae that are typically associated with *K. crouchii* along the rock ledges are *Crassula expansa* Dryand. subsp. *fragilis* (Baker) Toelken, *C. alba* Forssk., *C. setulosa* Harv. var. *longiciliata* Toelken and *Kalanchoe rotundifolia* (Haw.) Haw., whilst one also can expect to find *Aloe spicata* L.f., *Tetradenia galpinii* (N.E.Br.) Phillipson & C.F.Steyn, *Merwilla plumbea* (Lindl.) Speta and *Litanthus pusillus* Harv.

To date only about 100 plants are known from the type locality, which is threatened by plantation forestry activities that occur in immediate proximity. Our understanding of the extent of the population numbers, as well as of the full distribution range of *Kalanchoe crouchii* will clearly benefit from further surveys of suitable habitats in the vicinity of Pilgrim's Rest. That plants have historically been gathered on only a handful of occasions, always close to the type locality, indicates a high degree of localisation and natural rarity of this interesting species. It joins the ranks of some 30 other succulent taxa from ca. 8 families that are endemic to the Wolkberg Centre of Endemism (Van Wyk & Smith 2001).

Kalanchoe crouchii is very easy in cultivation. It works well as a small accent plant, but given its comparatively small stature, is best suited for growing in a container filled with a rich, well-drained soil mixture. When watering the plant, care should be taken not to wash off the white, waxy coating, which much adds to the charm of the species in cultivation. Whilst the species grows as well in dappled shade as in full sun, in fully exposed positions the leaves turn a distinct coppery-bronze.

FIGURE 3.—The reddish brown follicles of *Kalanchoe crouchii* split to appear star-shaped. They are brittle and enveloped in the dry, greyish brown remains of the calyx and corolla. Photograph: N.R. Crouch.

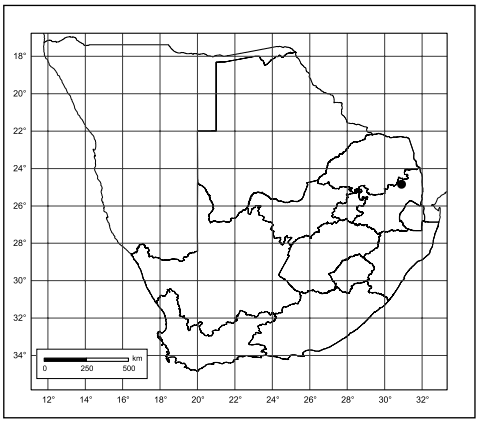

FIGURE 4.—Known geographical distribution range of *Kalanchoe crouchii* in South Africa.

FIGURE 5.—*Kalanchoe crouchii* occurs on the ledges (bottom right of the image) of dolomitic outcrops in north-facing grassland in the vicinity of Pilgrim's Rest. *Aloe spicata* grows at the top of the ridge. Photograph: N.R. Crouch.

Like all pseudo-rosulate kalanchoes with sessile, round leaves and dense, club-shaped inflorescences, plants signal early on when they approach reproductive maturity. The central axis starts elongating and the internodes become longer. Flowering events are usually initiated from April (autumn, southern hemisphere) through September, with the plants in full flower by early- to mid-winter (Figure 2), to fruit by November (Figure 3).

Description.—Perennial, few-leaved, solitary or with up to 5 rosettes, sparsely branched from near the base, plantlets formed higher up on the peduncle, glabrous, very waxy throughout, small to medium-sized succulent, 0.25(–0.40) m tall in bloom. *Stems* erect to slightly leaning and curved upwards, glabrous, very waxy especially along internodes, nearly white. *Leaves* opposite, erectly spreading, never floppy, succulent, sessile, concave to flattened above, convex below, glabrous, waxy, light grey to white; petiole absent; blade 450–500(–600) × 300–400(–500) mm, round to obovate, not folded lengthwise, occasionally lightly pink-infused, concave-bowl-shaped; axils sometimes carrying small leafy shoots and short branches that produce flowers in season; base narrow, not auriculate; apex rounded-obtuse, not truncate, not indented; margins smooth, same colour as blade, sometimes bronze. *Inflorescence* a slender, erect, sparsely to densely flowered, cylindrical thyrse consisting of several dichasia terminating in monochasia, 0.25(–0.35) m tall, dry inflorescence remaining on the plant for a long time; branching low down and higher up at internodes on round to 2-angled peduncle through production of side-shoots. *Flowers* 10–11 mm long, erect to slanted horizontally, pale yellowish green to greenish white (tube) and yellow (lobes), all parts excepting tepal lobes above covered with a substantial white waxy bloom, highly scented, resinous to the touch; pedicels 7–9 mm long. *Calyx* densely white-waxy, hardly contrasting against slightly paler light greenish yellow corolla tube; sepals 4, 3–4 mm

long, elongated-triangular, acute, apex rounded. *Corolla* white-waxy, light greenish yellow when wax removed; tube 9–10 mm long, quadrangular, 4-angled, narrowly elongated-urceolate, *lobes* 2–3 × 2 mm, almost square to slightly rectangular, margins not inrolled, apically truncated to distinctly indented, initially spreading at 90° from corolla tube, later recurved, bright yellow with an apical flush of brick red to one side of the midvein. *Stamens* 8, ± inserted in two ranks close to the mouth of the corolla tube, all exserted 1 mm; filaments 2.0–2.5 mm long, thin, light green, in two ranks, stamens with slightly longer filaments opposite corolla; anthers 0.4–0.6 mm long, yellow. *Pistil* ± pyriform, consisting of 4 carpels; ovaries 6 mm long, ± cylindrical, mid-green; styles ± 1.5–2.0 mm long; stigmas hardly capitate, light yellow, exserted as far as or slightly less than anthers; scales 1 × 1.0–1.5 mm, light yellow, narrowing towards the base, truncate to slightly bulged and repand above, contiguous, arranged in a virtually continuous ring. *Follicles* brittle, grass spikelet-like, reddish brown, enveloped in dry, reddish-brown remains of calyx and corolla which dry greyish-brown, splitting star-shaped, 6–7 mm long. *Seeds* 0.50–0.75 mm long, light to dark brown, nearly rectangular. *Chromosome number*: unknown. Plate 2366.

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PLATE 2367 *Kalanchoe manginii*

Kalanchoe manginii Crassulaceae: Kalanchooideae

Madagascar

Kalanchoe manginii, as 'mangini', Raym.-Hamet & H.Perrier in Ann. Sci. Nat., Bot. sér. 9,16: 370 (1912). Raymond-Hamet & Marnier-Lapostolle: 103, Plate XXXVI, Figures 124 and 125 (1964); Jacobsen: 287 (1977); Jacobsen: 618, Figure 867 (1986); Sajeva & Costanzo: 152 (1994); Boiteau & Allorge-Boiteau: 76 (1995); Rauh: 153, Figures 398 & 399 (1995); Springate: 180 (1995); Descoings: 164 (2003). *Bryophyllum manginii* (Raym.-Hamet & H.Perrier) Nothdurft: 96 (1962).

When the French naturalist Joseph Marie Henri [also spelled 'Henry'] Alfred ['Henri', the name he used] Perrier de la Bâthie (1873–1958) for the first time collected material of *Kalanchoe manginii* (Figure 1) in Madagascar, he could not have predicted how popular this species would become in global horticulture, additionally because of its very limited natural geographical distribution range. In mild climates plants are easy to keep outdoors, and in harsh climates plants thrive in greenhouses or even under the rather low-light conditions in closeted living rooms or kitchens. Regardless of the prevalent climate, *K. manginii* can truly be grown anywhere and it is furthermore near-perfect in its response to being cultivated in containers, especially as a hanging basket subject.

Moreover, hybrids of which *Kalanchoe manginii* is one parent have resulted in the global distribution of a range of selected cultivars that contain genetic material derived from Perrier de la Bâthie's find of exactly 110 years ago (Hamet & Perrier de la Bâthie 1912). Perhaps the best known of these cultivars is *K.* 'Tessa', which was purportedly derived from a hybrid between *K. gracilipes* (Baker) Baill. and *K. manginii*, and, along with *K. manginii* itself (Durrant 2020), remains horticulturally popular to this day. Remarkably, in the case of this hybrid the genus name *Kalanchoe* has become associated with 'Tessa', rather than 'Tessa' with *Kalanchoe* (Purveur & Harbour 1996)! Other *Kalanchoe* cultivars, such as *K. porphyrocalyx* (Baker) Baill. 'Wendy' (Smith & Shtein 2021), which shares aspects of the general growth form of *K. manginii* and *K.* 'Tessa', have similarly remained a mainstay of plants cultivated indoors in harsh-climate parts of the world (Merrick 2008; Shaw 2008). In the past, reference to *K.* 'Wendy' being a hybrid with the formula *K. miniata* × *K. porphyrocalyx* has been published by Springate (1995). Note though that, based on vegetative and reproductive morphological considerations, Smith & Shtein (2021) suggested that this entity, for which the cultivar name 'Wendy' is in use, might well be a selection of *K. porphyrocalyx*, the species, so yielding *K. porphyrocalyx* 'Wendy'.

In southern Africa a different cultivar, *Kalanchoe* 'Margrit's Magic' (Figure 2) (Smith et al. 2018), which is often mislabelled as *K.* 'Tessa' in the horticultural trade, has become even more popular than *K.* 'Tessa' in domestic gardening as it is more drought tolerant and generally hardier when grown outdoors. *Kalanchoe manginii* is also one parent of this cultivar,

PLATE 2367.—1, plant in flower, × 1.5; 2, apical view of perianth lobes, × 5; 3, side view of flower, × 5. Voucher specimen: *G.F. Smith & E. Figueiredo 59* in H.G.W.J. Schweickerdt Herbarium, Pretoria. Artist: Lesley Deysel.

FIGURE 1.—Habit of *Kalanchoe manginii*. Plants have thin, wiry stems and small, round to obovate leaves. The leaves take on a reddish brown colour when grown in full sun. Photograph: G.F. Smith.

which might have been derived from the same parentage from which *K.* 'Mirabella' was selected, i.e., *K. blossfeldiana* Poelln. × *K. manginii*.

Two further named cultivars derived from the hybrid with the formula *Kalanchoe blossfeldiana* × *K. manginii* are *K.* 'Happy Bells', which has pink (not red or reddish) flowers, and *K.* 'Maya', which has stubby, pinkish red flowers. Although the parentage of these cultivars was not previously disclosed (see Shaw 2008), both show the same growth form, omni-directional-disposed flowers, minutely hairy fertile parts, thin, woody stems, and the *K. manginii*-like leaf shape as observed in *K.* 'Margrit's Magic' and *K.* 'Mirabella'. Moreover, other than *K.* 'Tessa', at least one further cultivar has been derived from the combination *K. gracilipes* × *K. manginii*, which is the leathery-red-flowered and generally reddish brown leafed *K.* 'Mariko', also briefly mentioned in Shaw (2008). A hybrid with the formula *K. jongmansii* Raym.-Hamet & H.Perrier × *K. manginii*,

FIGURE 2.—*Kalanchoe manginii* is one of the parents of the cultivar *K.* 'Margrit's Magic'. Photograph: G.F. Smith.

notable for its orange flowers that are intermediate between the yellow and red flowers of its parents, respectively, is known as *K.* 'Orangery' Jankalski and also has been distributed internationally (Trager 2006). Finally, several hybrids between *K. manginii* and representatives of *K.* sect. *Alatae* Raym.-Hamet, for example, with the formula *K. manginii* × *K. uniflora* (Stapf) Raym.-Hamet exist in the plant trade in East Asia and Europe, although to the best of our knowledge these have not been given cultivar names. The flowers of a selection of these cultivars and associated hybrids are illustrated in Figure 3.

FIGURE 3.—Comparison of the flowers of *Kalanchoe manginii* and some hybrids derived from it that are available in the horticultural trade: a, *K. manginii*; b, *K.* 'Tessa'; c. *K.* 'Mariko'; d, a hybrid with *K. manginii* and *K. uniflora* as parents; e, *K.* 'Mirabella'; f, *K.* 'Maya'; g, *K.* 'Happy Bells'; h, a hybrid with *K. blossfeldiana* and *K. manginii* as parents. Photographs: R. Shtein.

FIGURE 4.—The leaves and stems of *Kalanchoe manginii* turn a reddish brown colour when exposed to direct sunlight. Photograph: G.F. Smith.

FIGURE 5.—The red, somewhat campanulate flowers of *Kalanchoe manginii* are, like the rest of the plant, finely pubescent. Photograph: G.F. Smith.

At present four subgenera are recognised in *Kalanchoe*: the geographically widespread autonymic one, as well as *K*. subg. *Bryophyllum* (Salisb.) Koord. and *K*. subg. *Kitchingia* (Baker) Gideon F.Sm. & Figueiredo that are both restricted to Madagascar, and the southern and south-tropical African *K*. subg. *Fernandesiae* Gideon F.Sm. (Smith & Figueiredo 2018; Smith et al. 2019; Smith 2020a). The subject of this paper, *Kalanchoe manginii*, which is endemic to Madagascar, is included in *K*. subg. *Bryophyllum* and has been successfully hybridised with representatives of three of the four currently recognised subgenera, i.e., the autonymic one, *K*. subg. *Bryophyllum* and *K*. subg. *Kitchingia*. As suggested by its production of clusters of small inflorescence bulbils as a reproductive mechanism (see discussion below) and mostly pendent flowers, *K. manginii* is included in *K*. subg. *Bryophyllum*. The presence of an indumentum, its colouration, and flower and stem morphology suggest a relationship with the recently described *K. rebmannii* Desc., which, along with *K. manginii* and *K. pubescens* Baker, all occur in east-central to southeastern Madagascar and may represent a series of species in which the gradual reduction in plant size is an adaptation to growing successfully at high elevations.

Kalanchoe manginii grows as small, leaning to creeping, multi-branched shrublets that generally do not reach a height of more than about 0.3 m. The thin, herbaceous to slightly woody stems are minutely pubescent while in the vegetative phase (Figure 4), becoming slightly more conspicuously so as they elongate into inflorescences. This trait is rather common in *Kalanchoe*, with *K. lanceolata* (illustrated as Plate 1848 in *Flowering Plants of Africa*; see Tölken 1982, with the same plate also having been used in Smith et al. 1997) being the best-known southern African species where the transition from smooth (vegetative growth lower down) to hairy (reproductive growth higher up) is considerably more marked than in *K. manginii*. The small, spathulate to obovate leaves, as well as inflorescences and flowers of the species are also minutely pubescent. The inflorescences are borne terminally and carry only a few large, bright red, pendent to very slightly horizontally-disposed flowers (Figure 5). The strikingly beautiful flowers are bell-shaped and in South Africa have prompted the Afrikaans common name *rooi klokkies*, which translates into English as 'red bells'. Like virtually all

kalanchoes, *K. manginii* is a short-day plant and flowers most prolifically during the winter and spring months (see for example https://www.greenhousegrower.com/crops/basics-beyond-new-kalanchoe-for-cultivation/#Tinsel/64513/1), from May to September (southern hemisphere).

Once the flowers of *Kalanchoe manginii* become wilted post-anthesis, the inflorescences carry clusters of small, densely arranged bulbils (Figure 6). Several kalanchoes use multiple asexual reproductive mechanisms, with the production of bulbils on leaf margins and desiccating inflorescences being a common occurrence, especially among taxa from Madagascar (see for example Friedmann 1975). However, while most kalanchoes only produce one to few, large bulbils per inflorescence node post-anthesis, *K. manginii* and other representatives of '*K.* subsect. *Pubescentes*', as well as of '*K.* subsect. *Campanulatae*', and some representatives of '*K.* subsect. *Proliferae*' produce dense clusters of bulbils on multiple inflorescence nodes. In these instances each bulbil is small in size, so perhaps aiding in their dispersal. Note: none of the infrageneric designations mentioned above were validly published. Of these small-bulbil producers, only representatives of '*K.* subsect. *Proliferae*' also develop bulbils on the margins of a leaf blade, which is a separate phenomenon, and usually contributes to these species being more prone to becoming invasive in places well away from their natural geographical distribution ranges (see for example Herrando-Moraira et al. 2020). Moreover, material of most kalanchoes will additionally easily strike root from severed leaves or even pieces of leaves, which has further contributed to some taxa becoming weedy (Smith & Figueiredo 2017; Smith 2019).

FIGURE 6.—Post-anthesis, clusters of densely arranged bulbils develop on the inflorescences of *Kalanchoe manginii*. Photograph: G.F. Smith.

Note that, with the exception of *Kalanchoe* 'Orangery', of which *K. manginii* is one parent and *K. jongmansii* the other, none of the hybrids and cultivars mentioned in this paper (see above) produces clusters of small bulbils. As *K. jongmansii* also produces such bulbil clusters, this seems to be a recessive reproductive trait.

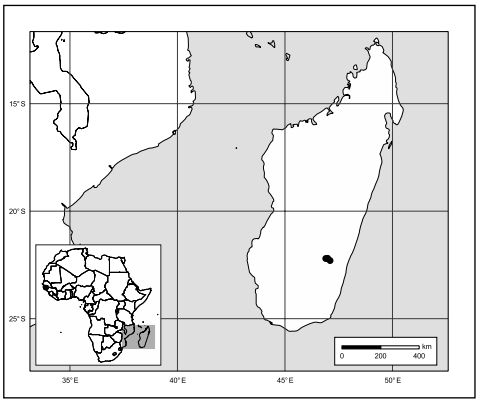

FIGURE 7.—Geographical distribution range of *Kalanchoe manginii* in east-central Madagascar based on information held in the Global Biodiversity Information Facility and specimens held at Herb. P, the herbarium of the Muséum national d'Histoire naturelle.

FIGURE 8.—The leaves of *Kalanchoe manginii* are bright green when plants grow in shade. Photograph: G.F. Smith.

When publishing the name *Kalanchoe manginii*, Hamet & Perrier de la Bâthie (1912) inter alia stated: 'Cette plante […] a été récoltée par M. Perrier de la Bâthie, en septembre 1911, sur les rocailles du versant ouest du massif d'Andringitra, à environ 1.800 mètres d'altitude.' In English: 'This plant […] was collected by Mr Perrier de la Bâthie, in September 1911, on rocks on the western slope of the Andringitra Massif [in east-central Madagascar], at about 1 800 metres above sea level.' (Figure 7). In the Andringitra Mountains in east-central Madagascar (see Baena et al. 2007; Boiteau & Allorge-Boiteau 1995; Allorge-Boiteau 1996), *K. manginii* often grows as a litho- or epiphyte and was treated as a montane (cloud) forest species by Rauh (1995). This already hints at the best way of cultivating plants of *K. manginii*. Plants thrive in shaded positions and also do well when exposed to direct solar irradiation; in the shade the leaves are a bright green colour (Figure 8) while in more sunny situations will become strongly reddish brown-bronze infused (Figures 1 and 4). Plants grow best in a friable, well-drained soil mixture that is high in humic content and kept moist. Since its discovery, no other occurrences of *K. manginii* have been documented, and the species can only be found in its natural habitat in the high elevation regions of the Andringitra Massif.

The specific epithet, *manginii*, commemorates Prof. Louis-Alexandre Mangin (8 September 1852–27 January 1937), who was Director of the Muséum national d'Histoire naturelle in Paris, France, from 1919 to 1931, so extending at least Raymond-Hamet's, if not Perrier de la Bâthie's, penchant for naming plants after people (Smith 2020b). Although Boiteau & Mannoni (1948) proposed the name *K. manginii* var. *triploidea* for a naturally occurring triploid of the species (see Jacobsen 1977, 1986; Rauh 1995) this designation was not validly published, although it is often presented as a synonym of the name *K. manginii*.

Description.—Perennial, tuft-like, later leaning to creeping, finely pubescent, sparsely to much-branched shrublets, with small, untidily rounded canopies, succulent, to 30–40 mm tall. *Stems* numerous, thin, flimsy, reddish-brown, ± erect to leaning, woody basally; leaf scars obvious, protruding. *Leaves* many, persistent along length of stems, sparsely arranged throughout, semi-erect to slanted away from branches at a 90° angle, succulent, finely pubescent, subsessile, flat, depressed along midrib, light to dark green or variously reddish brown-bronze infused, not waxy; petiole indistinct; blade succulent, 15–30 × 10–20 mm, obovate to spathulate to, more rarely, oblong to orbicular; base narrow, cuneate; apex rounded-obtuse; margins entire, concolourous or faintly red-infused, not bulbiliferous. *Inflorescence* a terminal, apically branched, few- and laxly-flowered compound dichasium, ± 50 mm long, drooping, bulbiliferous, producing dense, early-developing bulbil clusters that subduct the flowers; peduncle short, tomentose, ± 5(–10–20) mm long, deep brownish red. *Flowers* 20–25 mm long, inside of corolla tube and lobes light yellow adorned with contrasting deep red veins, pendent, campanulate, finely pubescent, subtended by small succulent bracts, waxy bloom absent; pedicels finely pubescent, 12–30 mm long. *Calyx* green to reddish green, basally very slightly fused; sepals 4, fused for < 1 mm, 5–9 mm long, free portion ovate to oblong, acute, curved away from the corolla tube at an angle of up to 45°, very finely pubescent. *Corolla* yellowish green in bud, eventually orange-red to deep crimson red, light green basally at maturity especially towards and where obscured by calyx, recurved lobes very slightly pubescent, waxy bloom absent; tube 18–23 mm long, campanulate, ± 4-angled before maturing, faintly pubescent on both surfaces, gradually expanding around the carpels, distinctly inflated in the apical half, somewhat constricted where the lobes fuse; lobes ± 4–5 × 6–7 mm, yellowish with prominent red veins inside, horizontally, ovate, apically obtuse-rounded with a slight indentation, minutely apiculate. *Stamens* inserted very low-down in corolla tube at ± lower end of carpels, 4 included, 4 slightly exserted; filaments 20–25 mm long, of two similar lengths, thin, light yellowish green, lightly infused with purple; anthers ± 1 mm long, greyish black; pollen yellow. *Pistil* consisting of 4 carpels; carpels 8–10 mm long, light shiny green, convergent, ovate, cuneate towards the styles; styles 15–17 mm long; stigmas capitate, white, included; scales ± vertically rectangular, free, ± 2 × 1 mm, light green, round-tipped above. *Follicles* not seen. *Seeds* not seen. *Chromosome number*: $2n = 34$ (Friedmann 1971). Plate 2367.

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Kalanchoe millotii Crassulaceae: Kalanchooideae

Madagascar

Kalanchoe millotii *Raym.-Hamet & H.Perrier* in Ann. Sci. Nat., Bot. sér. 9, 16: 374 (1912); Raymond-Hamet & Marnier-Lapostolle: 36, Plate X, Figure 26, Plate XI, Figures 27, 28 (1964); Jacobsen: 287, Plate 105, Figure 2 (1977); Jacobsen: 620, Figure 871 (1986); Sajeva & Costanzo: 152, bottom right (1994); Allorge-Boiteau: 12, 17 (1995); Boiteau & Allorge-Boiteau: 159, 160 (1995); Rauh: 116 (1995); Rauh: 304, 309, 311, Figures 1146–1151 (1998); Descoings: 166 (2003); Smith & Figueiredo: 80 (2019).

The genus *Kalanchoe* Adans. has differentiated extensively in Madagascar, where about 50% of the ca. 150 species included in the genus globally are endemic. Three of the four subgenera recognised in *Kalanchoe*, *K.* subg. *Kalanchoe*, *K.* subg. *Bryophyllum* (Salisb.) Koord. and *K.* subg. *Kitchingia* (Baker) Gideon F.Sm. & Figueiredo are represented in Madagascar. Only two endemic Madagascan species are included in *K.* subg. *Kitchingia*, with the rest of the species distributed between the other two subgenera recognised at present, with slightly more species included in *K.* subg. *Bryophyllum* than in *K.* subg. *Kalanchoe*.

In Madagascar, in especially *Kalanchoe* subg. *Kalanchoe*, a number of species are extensively and conspicuously covered by fine, velvety hairs, while in others the tomentum can be quite coarse. The best known of these species are *K. beharensis* Drake and *K. tomentosa* Baker, both of which are very common in succulent plant collections and amenity horticulture. *Kalanchoe millotii*, the subject of this paper, is a small, shrubby species from Madagascar and also has most of its organs covered by a fine tomentum (Figure 1). Of these three related taxa, *K. beharensis* is arborescent and can grow to a height of 2–3 m; *K. tomentosa* is a small to medium-sized, often scraggly, shrub that can reach a height of 1 m; and *K. millotii* is a small shrub that hardly exceeds 0.5 m in height when in flower and it generally develops into tidy, irregularly rounded bushes. Predictably, in South Africa the species is known as *fluweelplakkie* in Afrikaans, and as velvet kalanchoe in English, both names alluding to the tomentose character.

Certain other 'fuzzy' Crassulaceae have become popular with gardeners and succulent enthusiasts, and include the South African *Cotyledon tomentosa* Harv. and several species of *Echeveria* DC., such as the Mexican *E. setosa* Rose & J.A.Purpus. This character trait – hairiness – is also seen in some succulents in other families such as the Commelinaceae and Asteraceae, with the likes of *Tradescantia silamontana* Matuda and *Caputia medleywoodii* (Hutch.) B.Nord. & Pelser, respectively. Fat-leaved and -bodied plants additionally endowed with a tomentum, therefore, not only employ succulence to store water in their tissues as a survival mechanism (MacDougal & Spalding 1910), but also adopt hairiness as a means to increase reflectivity of high solar irradiation. It is further speculated that air movement is restricted in the immediate vicinity of stomata, so resulting in water loss

PLATE 2368.—1, inflorescence, × 0.75; 2, side view of flower, × 1.25; 3, apical view of perianth lobes, × 1.5; 4, adaxial view of leaf, × 1; 5, habit, × 0.75. Voucher specimen: *G.F. Smith 1078* in H.G.W.J. Schweickerdt Herbarium, Pretoria. Artist: Lesley Deysel.

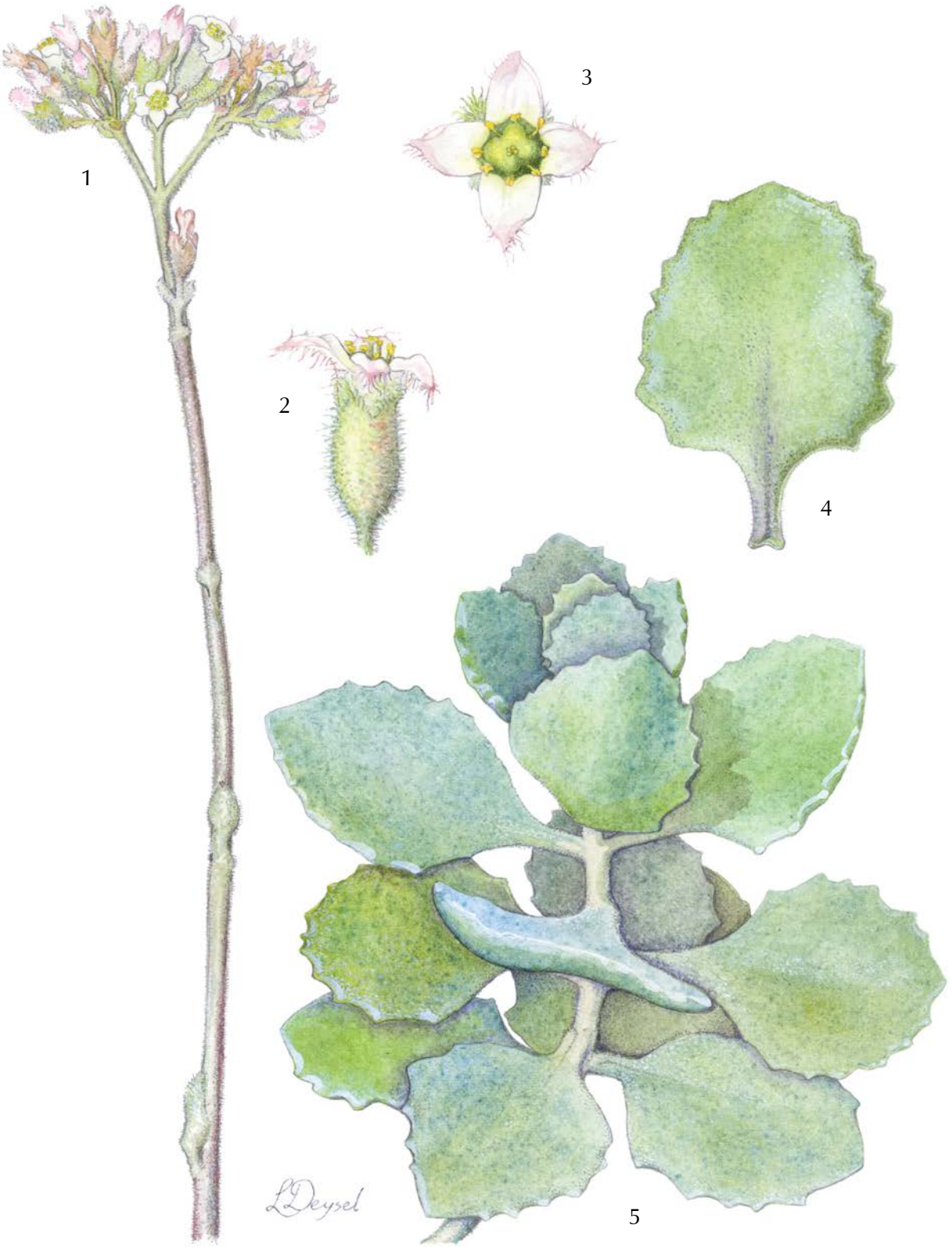

PLATE 2368 *Kalanchoe millotii*

FIGURE 1.—*Kalanchoe millotii* is a small to medium-sized shrub, typically not exceeding about 400 mm in height when not in flower. All the plant parts are noticeably covered by fine, velvety hairs. Photograph: G.F. Smith.

being arrested, and that the hairs also cast a protective, cooling shade on the leaves that bear them (Von Willert et al. 1992).

Both *Kalanchoe beharensis* and *K. tomentosa* are extremely variable and several cultivars with desirable characters have been named in these two species. In contrast, *K. millotii* is much more constant in the expression of its characters and no horticultural selections have yet been named. However, *K. millotii* has been used as one parent in at least two hybrids of horticultural origin. The first of these, *K.* ×*hummeliae* Gideon F.Sm. (Smith 2020a), is a hybrid between *K. beharensis* and *K. millotii* (Figure 2) with the California-produced cultivar *Kalanchoe* 'Fern Leaf' H.Johnson (Johnson

FIGURE 2.—*Kalanchoe* ×*hummeliae*, a hybrid between *K. beharensis* and *K. millotii*, is also densely tomentose. The leaves are larger than those of *K. millotii* and usually more deeply incised along the margins. Photograph: G.F. Smith.

FIGURE 3.—*Kalanchoe* ×*gildenhuysii* has *K. millotii* and *K. tomentosa* as parents. Photograph: G.F. Smith.

Cactus Gardens 1961) being derived from it. *Kalanchoe* ×*hummeliae* was named for Minnie Belle Hummel [née Byrne] (14 April 1904 [Piedmont, Wyoming, USA]–15 January 1993), who, with her husband, Edward Charles Hummel, (18 July 1903 [Prosperity, Missouri, USA]–29 November 1979), operated a family-owned nursery for more than 40 years, from 1935 until 1978 (Mitich 1993).

The second nothospecies, *Kalanchoe* ×*gildenhuysii* Gideon F.Sm. & Figueiredo (Smith & Figueiredo 2020), which was recorded from South Africa, has the two Madagascan species, *K. millotii* and *K. tomentosa*, as parents (Figure 3). The likelihood is not low, however, that these two hybrids, *K.* ×*hummeliae* and *K.* ×*gildenhuysii*, have been created deliberately or arose by chance more than once in different parts of the world, given the popularity of the parent species in cultivation.

With plants of *Kalanchoe beharensis*, *K. millotii*, and *K. tomentosa* being tomentose, this character is also very much evident in the case of both *K.* ×*hummeliae* and *K.* ×*gildenhuysii*, with especially the leaves and stems, as well as the flowers, of these nothospecies covered with fine hairs. *Kalanchoe* ×*hummeliae* generally grows as medium-sized, thin-stemmed, tree-like shrubs that are smaller than the arborescent *K. beharensis*, but larger than *K. millotii*, while *K.* ×*gildenhuysii* remains lower growing, reaching a height of about 0.5 m, similar to that of *K. millotii*.

Material that was eventually described as *Kalanchoe millotii* was first collected by 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]) in July 1910 in central southwestern Madagascar (Hamet & Perrier de la Bâthie 1912). 'Henri' or 'Henry' Perrier de la Bâthie was an indefatigable collector of natural history specimens in Madagascar (Dorr 1997). On several occasions between the 1890s and 1930s he visited the island, which was a French colony from 1896 until it gained independence in 1960, and inter alia amassed a substantial herbarium that was donated to the Muséum national d'Histoire naturelle in Paris, France, in 1930. Perrier de la Bâthie had more than a passing interest in *Kalanchoe* and between 1923 and 1928 he described, as sole author, 11 new species in the genus. Earlier, from 1912 to 1915, he briefly 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. Raymond-Hamet had a distinct preference to commemorate people in the specific epithets he chose for new species he described; however, he never honoured his collaborator, Perrier de la Bâthie, in this way.

In contrast, Perrier de la Bâthie consistently named his 11 solely-authored new kalanchoes for what he interpreted as prominent morphological characters of the plants, or named them after the locations from which they were collected (Smith 2020b). Perrier de la Bâthie is, however, commemorated in the small-growing *Aloe perrieri* Reynolds, in the Asphodelaceae subfam. Alooideae, as well as in the giant succulent tree *Adansonia perrieri* Capuron (Malvaceae), both endemic to Madagascar. These two commemorations recognise Perrier de la Bâthie's contributions to the taxonomy of Madagascan *Aloe* and *Adansonia*, for he authored several species in both genera.

FIGURE 4.—The leaves of *Kalanchoe millotii* are densely tomentose, and have a light green to glaucous colour. Photograph: G.F. Smith.

Hamet & Perrier de la Bâthie (1912) named *K. millotii* for Monsieur Adolphe Philippe Millot (1 May 1857–18 December 1921), a botanical and zoological artist (originally given in French as: 'professeur de dessin') at the Muséum national d'Histoire naturelle in Paris. It is appropriate to include in the pages of *Flowering Plants of Africa*, a scientific journal that has actively promoted botanical art for more than a century, a plate of a species that was named for a botanical artist who died exactly 100 years ago. Note that the widely cultivated Madagascan succulents *Aloe millotii* Reynolds (Asphodelaceae: Alooideae) and *Euphorbia millotii* Ursch & Leandri (Euphorbiaceae) were named for a different Millot, Prof. Jacques Millot (9 July 1897–23 January 1980).

Plants of *Kalanchoe millotii* have an overall dull light green to glaucous green appearance that results from the fine tomentum with which it is covered (Figure 4). The leaves remain more or less flat, and the leaf margins are irregularly toothed (Figure 5). The petals are dull-coloured – bright white through pale yellowish green- to pinkish- to yellowish orange-infused (Figures 6 and 7). The light green, tomentose calyx of *K. millotii* obscures much of the corolla tube (Figure 7), a character shared with *K. beharensis* but not with *K. tomentosa*. A further Madagascan *Kalanchoe* species, *K. orgyalis* Baker, sports a variously copper-coloured tomentum on, especially, young leaves, and bright yellow flowers and free, thickly succulent, deltoid-triangular sepals that project from the corolla tube at a 90° angle. *Kalanchoe orgyalis*, therefore, cannot be confused with the light green to glaucous *K. millotii* (Figures 8 and 9).

FIGURE 5.—The leaf margins of *Kalanchoe millotii* are irregularly toothed and the leaf blades remain more or less flat. Photograph: G.F. Smith.

FIGURE 6.—Flowers of *Kalanchoe millotii* are dull coloured, in the case of this form white infused with pink. At maturity the corolla lobes are recurved. Photograph: G.F. Smith.

No infraspecific taxa are today recognised in *Kalanchoe millotii*, even though Humbert (1933) published *K. millotii* subsp. *brevisepala* Humbert. However, this subspecies is today included in the synonymy of *K. dinklagei* Rauh (Rauh 1985; Smith et al. 2019), along with *K. brevisepala* (Humbert) L.Allorge (Allorge-Boiteau 1995).

FIGURE 7.—This form of *Kalanchoe millotii* has pure white corolla lobes. The tomentose calyx obscures much of the corolla tube. Photograph: G.F. Smith.

Kalanchoe millotii is propagated through stem and branch cuttings that will root easily in a well-drained, friable soil mixture. Plants require very little watering and do well when grown in full or filtered sunlight. When grown in sunny positions, the leaves will soon take on a subtle, golden hue (Figure 10). When grown in dappled shade the leaves tend to remain greyish green. With its finely velvety leaves, *K. millotii* is a worthy addition to a waterwise garden. However, plants are not cold-hardy and a heavy frost will kill them.

As is the case with most species of *Kalanchoe*, the flowering of *K. millotii*

generally peaks in mid-winter. However, at least some forms of the species flower in mid-summer, from November to January (southern hemisphere), with a peak in December.

Kalanchoe millotii occurs in southern Madagascar (Boiteau & Allorge-Boiteau 1995; Allorge-Boiteau 1996) (Figure 11). Hamet & Perrier de la Bâthie (1912) first recorded the species from rocks, bare sandstone and volcanic rocks at an altitude of about 400 m above sea level on Mount Vohibory, ca. 50 km due north of Fotadrevo in the district of Ampanihy in south-central Madagascar.

Description.—Perennial, sparsely to usually densely branched succulent shrubs, with irregularly rounded canopies, 0.3–0.4(–0.5 when in flower) m tall. *Stem* branched from the base, thin, to 5–9 mm

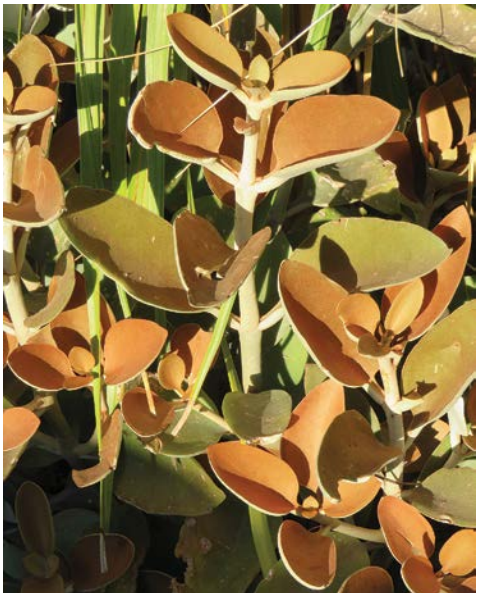

FIGURE 8.—Especially the young leaves of *Kalanchoe orgyalis* are covered by a very fine, copper-coloured tomentum. Photograph: G.F. Smith.

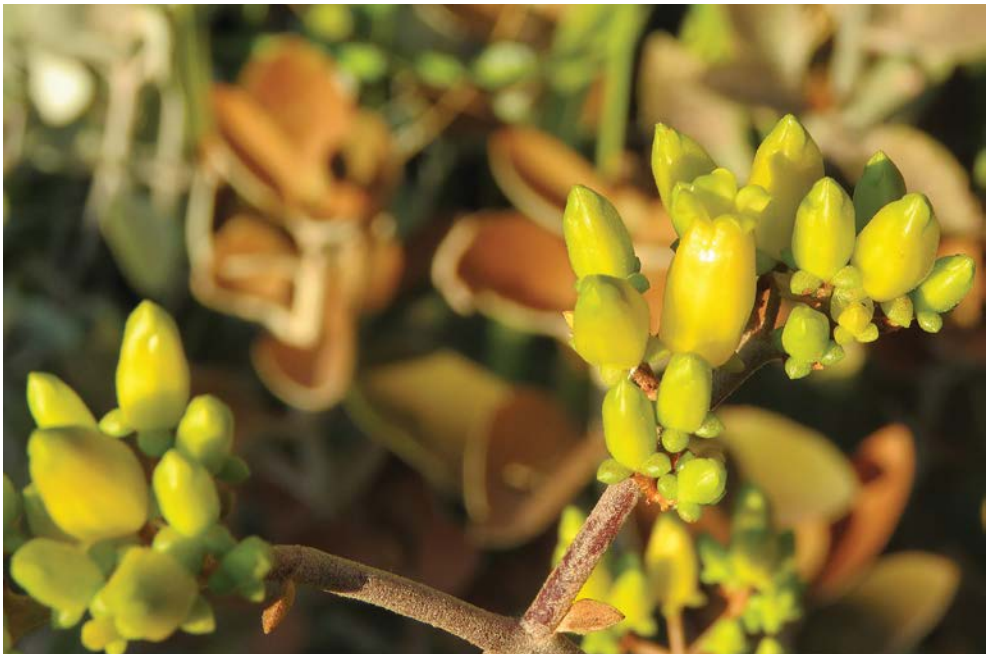

FIGURE 9.—The corollas of *Kalanchoe orgyalis* are generally golden yellow and subtended by small, stubby sepals. Photograph: G.F. Smith.

FIGURE 10.—When growing in full sun, the leaves of *Kalanchoe millotii* take on a golden hue. Photograph: G.F. Smith.

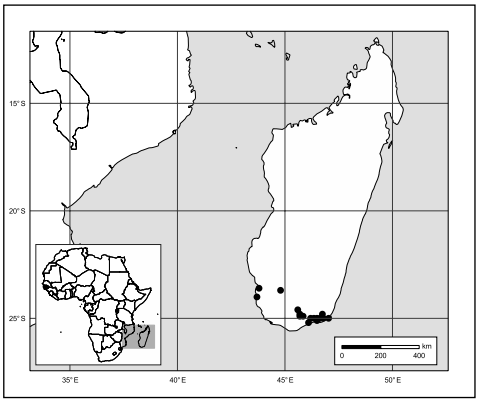

FIGURE 11.—Geographical distribution range of *Kalanchoe millotii* in Madagascar.

in diameter, ± erect or variously curved outwards to leaning, surface prominently and densely covered by fine, velvety hairs, leaf scars obvious, light greyish to greenish white. *Leaves* dull light green to glaucous-green to grey-green, decussate, laxly arranged, few to many especially towards terminal half to two-thirds of branches, slowly shed lower down to yield small leaf scars, erect when young to variously spreading at maturity, succulent, densely pubescent, petiolate, ± flattened above and below; petiole 5–15(–20) mm long, same colour as leaf blade, succulent, distinctly grooved above, groove extending into blade, basally not or hardly enlarged; blade 30–60 × 30–60 mm, ovate to obovate to nearly orbicular, flat, succulent; base cuneate; apex rounded-obtuse but always acute-tipped; margins flat to very slightly down-curved in older leaves, irregularly sinuate-dentate, teeth broad but always acute-tipped, usually concolorous, transitional leaves on flowering stems lacking teeth. *Inflorescence* a terminal, densely or, rarely, laxly branched, few- to many-flowered corymb, up to 200 mm long, rounded, erect to gracefully leaning sideways and upwards; pedicels 3–12 mm long, stout, densely pubescent. *Flowers* pure, bright white to pale yellowish green- to yellowish orange-infused, waxy bloom absent, ± erect or slanted in various directions, densely pubescent except adaxial surfaces of petal lobes; *calyx* dull glaucous green to yellowish green- to orange-infused; sepals 5–7 mm long, elongated-triangular, fused below for ± 1 mm, acute, glandular-hairy, obscuring the corolla tube; corolla tube 6–8 mm long, cylindrical, more or less quadrangular-urceolate to slightly campanulate, slightly tapering to the mouth, scarcely 4-angled; lobes 2 × 2 mm, ± square, strongly recurved at maturity, indented at the tips, not apiculate, bright white to yellowish green- to yellowish orange-infused, or pinkish. *Stamens* inserted high up above middle of corolla tube, ± 1 mm exserted; filaments ± 4 mm long, thin, light yellowish green; anthers ± 0.50–0.75 mm long, yellow, exserted. *Pistil* consisting of 4 carpels; carpels 3–4 mm long, light yellowish green; styles 2.0–2.5 mm long; stigmas light yellowish green, very slightly capitate; scales ± trapeziform to square-globular, connate to hardly connate, ± 1 × 1 mm, slightly apiculate above. *Follicles* 5–7 mm long, light green when young, lower down enveloped in dry,

greyish brown remains of corolla, drying dark brown, splitting star-like, calyx at first remaining green and closely adhering to follicles. *Seeds* 0.75–1.00 mm long, dark reddish brown to dark brown, cylindrical to club-shaped to slightly banana-curved. *Chromosome number*: $2n = 38$? (Friedmann 1971). Plate 2368.

ACKNOWLEDGEMENTS

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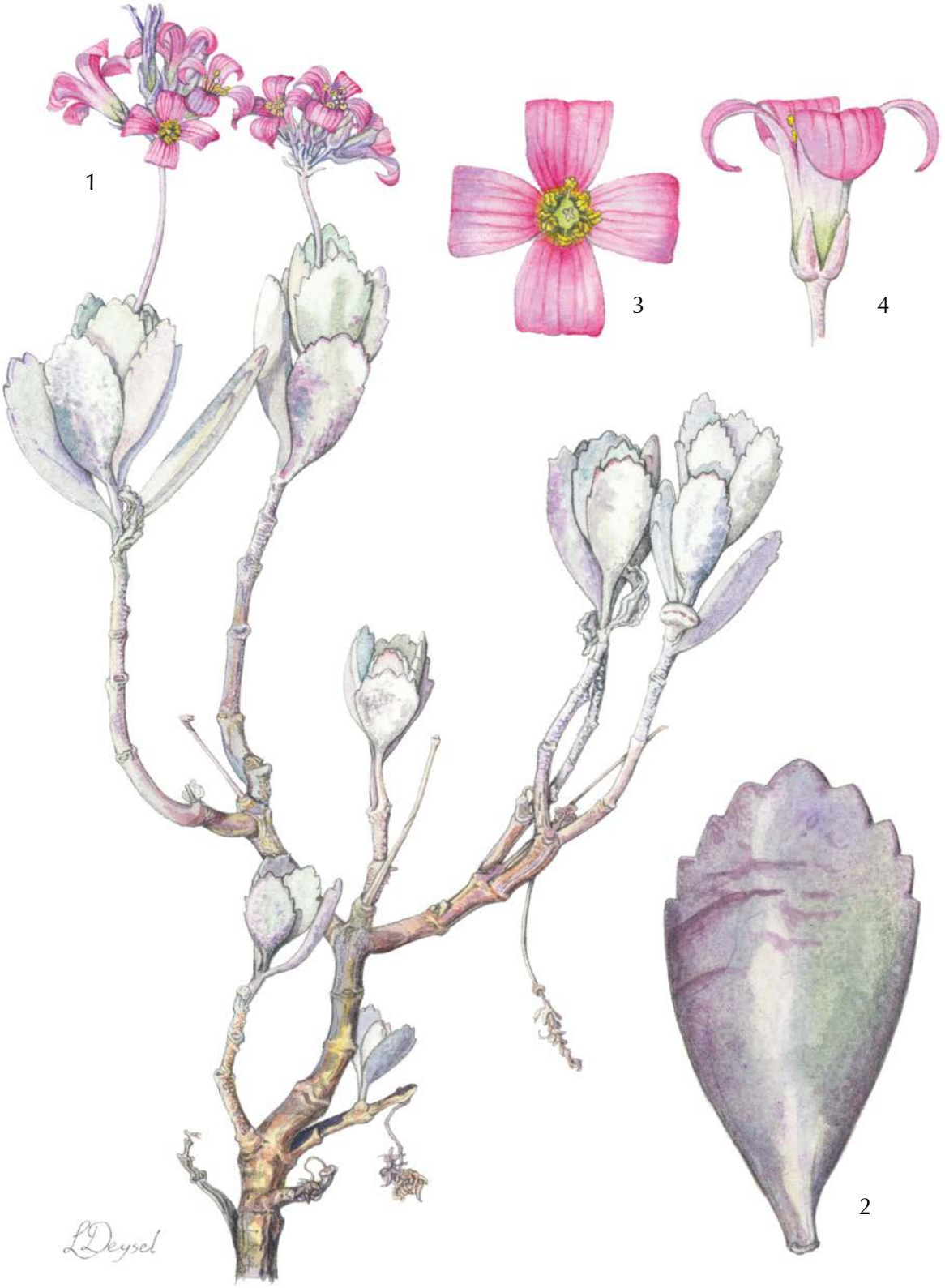

PLATE 2369 *Kalanchoe pumila*

Kalanchoe pumila Crassulaceae: Kalanchooideae

Madagascar

Kalanchoe pumila *Baker* in J. Linn. Soc., Bot. 20: 139 (1883). Hamet: 25 (1908); Raymond-Hamet & Marnier-Lapostolle: 21, Plate VI, Figures 11–12 (1964); Jacobsen: 289 (1977); Jacobsen: 626, Figure 882 (1986); Boiteau & Allorge-Boiteau: 173–174 (1995); Rauh: 92, Figure 222, 116, 157–158, Figures 413–416 (1995); Brickell: 578 (1998); Brickell: 594 (2003); Descoings: 171 (2003); Bryant et al. 741 (2005); Smith et al.: 296 (2019). *Kalanchoe multiceps* Baill.: 469 (1885). *Kalanchoe brevicaulis* Baker: 470 (1887). *Kalanchoe pumila* f. *venustior* Boiteau, in Boiteau & Allorge-Boiteau: 175 (1995).

A popular way in which horticultural companies, retail plant nurseries, and commercial garden centres entice the purchasing public to acquire decorative plants for households and office spaces is to strategically place comparatively affordable, potted flowering material at or near check-out lines. Given the ease with which material of *Kalanchoe* Adans. can be manipulated to flower at any time of year – plants respond to day length (see Smith et al. 2019: 97–98, 282–284 for a discussion) – a number of species, hybrids and cultivars have become exceedingly popular at outlets offering such impulse purchases. For example, since at least the 1990s very short, rooted, profusely flowering shoots of selections and hybrids of the Madagascan *K. blossfeldiana* Poelln., popularly known as 'Flaming Katy' or 'Florist's kalanchoe', are readily available in the horti- and floricultural trades (Figure 1), and even in supermarkets that do not otherwise sell plant material (Bloemen Bureau Holland 1999/2000; Flower Council of Holland 2004) (Figure 2). However, there is a catch: the general quality of material of *K. blossfeldiana* and its cultivars tends to deteriorate over time, with the flowering event often becoming considerably less substantial in later flowering seasons. Luckily for customers, acquiring fresh, shop-bought flowering kalanchoes such as *K. blossfeldiana*, is easily achieved.

Kalanchoe pumila (Figure 3), the subject of this paper, has also become very popular as material for impulse purchases, and additionally has been used as one parent in producing some strikingly beautiful hybrids with *K. blossfeldiana* that are sold in florist shops and plant nurseries, generally simply under the name 'Kalanchoe'.

This journal, *Flowering Plants of Africa* (*FPA*), started out as *Flowering Plants of South Africa* in 1920, but from volume 25 (1945, published in 1946) onwards was renamed *Flowering Plants of Africa*, for a while with '*The*' before '*Flowering*' as part of the title, so broadening the scope of the material that qualifies for inclusion (Killick & Du Plessis, no date). In addition, for the purposes of *FPA*, Madagascar forms part of the concept of what constitutes 'Africa'. Since 1946 numerous Madagascan species have been illustrated in the pages of the journal. However, up to 2019 only three Madagascan *Kalanchoe* species, *K. tubiflora* (Harv.) Raym.-Hamet (as *Bryophyllum delagoense* (Eckl. & Zeyh.) Schinz), *K. beauverdii*

PLATE 2369.—1, whole plant, × 1; 2, adaxial leaf surface, × 3; 3, apical view of a flower, × 3; 4, side view of flower, × 3. Voucher specimen: *G.F. Smith 1085* in H.G.W.J. Schweickerdt Herbarium, Pretoria. Artist: Lesley Deysel.

FIGURE 1.—'Kalanchoe Mini' plants sold in multi-coloured cellophane sleeves in Alcanena, Portugal, near the cash registers of a grocery store. Photograph: G.F. Smith.

FIGURE 2.—Potted *Kalanchoe blossfeldiana* cultivars offered for sale by a florist shop in Alcanena, Portugal. Photograph: G.F. Smith.

Raym.-Hamet (as *Bryophyllum beauverdii* A.Berger; however, the material illustrated likely represents *K. scandens* H.Perrier, a closely related species, see Shtein & Smith 2021: 94–95, 113) and *K. gastonis-bonnieri* Raym.-Hamet & H.Perrier (Smith et al. 2020) have been featured (Table 1). Now, in its 101st year, this situation is to some extent rectified, with a further six species, *K. beharensis* Drake, *K. crouchii* Gideon F.Sm. & Figueiredo, *K. manginii* Raym.-Hamet & H.Perrier, *K. millotii* Raym.-Hamet & H.Perrier, *K. pumila* and *K. serrata* Mannoni & Boiteau, all from Madagascar except *K. crouchii*, discussed and illustrated in this issue.

For the past century, *FPA* has been the primary journal dealing with and promoting botanical art in continental Africa (see for example Arnold 2001). A range of botanical artists has contributed to the 2380 plates published in *FPA*, including of kalanchoes, with seven (that is, a third) of the kalanchoe plates having been done by Gillian [Gill] Condy, formerly the resident botanical artist of the South African National Biodiversity Institute (see the dedication of volume 66 of *FPA*). This 67th volume introduces a further artist, Dr Lesley Deysel (Figure 4), to the readership of this journal; she painted four of the kalanchoes for this volume (Table 1). Lesley Claire Frances Deysel née Barker (born Cape Town, 9 April 1983–) is the grand-niece of botanist and botanical artist Winsome Fanny Barker (born Jamestown, 23 September 1907–died Cape Town, 27 December 1994), a former curator of the Compton Herbarium in Kirstenbosch, Cape Town. Lesley studied archaeology and ancient languages at the University of Pretoria and received a D.Litt. in ancient Hebrew in 2017. From 1995 she was taught art by painter and biological illustrator Elbie de Meillon, and joined the Botanical Artists Association of Southern Africa in 2009 after attending a workshop presented by Gill Condy. She has illustrated a number of journal articles, particularly on species of *Euphorbia* L., and several dissertations. She works in both pen-and-ink and watercolour, makes contemporary art in various media, and also does archaeological illustrations. When not drawing or painting she may be found lecturing medical terminology at the University of Pretoria, participating in an archaeological dig, or working at Pretoria's Trent Gallery.

FIGURE 3.—*Kalanchoe pumila* grown as a groundcover outside the Royal Exhibition Building and Carlton Gardens, Melbourne, Australia. Photograph: G.F. Smith.

Up to and including this volume, number 67, of *FPA*, 22 plates of kalanchoes, about 10% of the number of species recognised in the genus, have appeared in the pages of the journal (Table 1). Ten of the taxa illustrated to date are indigenous to southern Africa, two are of species from further north in Africa, two are Socotran in origin and eight depict Madagascan species.

Kalanchoe pumila is easy to identify given its low-growing stature; the dense, white, floury wax coating on its purplish pink leaves (Figure 5); and the clusters of large, erectly borne to spreading, light (Figure 6) to purplish pink (Figure 7) flowers that appear from mid- to late-winter to spring and early-summer (August to October in the southern hemisphere). The white wax coating is much more prominent on the youngest leaves, so affording them considerable protection against possible

FIGURE 4.—Botanical artist Lesley Deysel née Barker (1983–) who painted four of the *Kalanchoe* species (*K. manginii*, *K. millotii*, *K. serrata*, *K. pumila*) that appear in this volume of *Flowering Plants of Africa*. Photograph: Munro J. Deysel.

TABLE 1.—Chronology of southern African, other African, Socotran and Madagascan *Kalanchoe* taxa illustrated in *Flowering Plants of South Africa* and (*The*) *Flowering Plants of Africa* up to 2021 (volume 67). Table updated from Smith et al. (2019). The name under which the species was illustrated, if no longer the one widely used, is given in parentheses in the second column

#	Taxon of *Kalanchoe*	Volume #	Plate #	Artist	Author(s)	Date
Indigenous southern African taxa						
1.	*K. thyrsiflora*	9	341	Cythna Letty	E.P. Phillips	July 1929
2.	*K. crundallii*	25	967	E. (Edith) K. Burges	I.C. Verdoorn	January 1945*
3.	*K. paniculata*	26	1007	R. Brown**	R.A. Dyer	January 1947
4.	*K. laciniata* (=*K. brachycalyx*)	27	1052	Artist not stated	E.A. Bruce	January 1949
5.	*K. lanceolata*	47***	1848	Rita Weber	H.R. Tölken	September 1982
6.	*K. sexangularis* var. *sexangularis*	47	1878	Rosemary Holcroft	H.R. Tölken	June 1983
7.	*K. crenata* subsp. *crenata*	61	2249	Gill Condy	N.R. Crouch & G.F. Smith	June 2009
8.	*K. leblanciae*	65	2328	Gill Condy	G.F. Smith, E. Figueiredo & N.R. Crouch	June 2017
9	*K. winteri*	66	2348	Gill Condy	G.F. Smith, E. Figueiredo & N.R. Crouch	June 2019
10.	*K. crouchii*	67	2366	Angela Beaumont	G.F. Smith, N.R. Crouch & E. Figueiredo	June 2021
Other mainland African species						
11.	*K. marmorata*	27	1049	Edith K. Burges	E.A. Bruce	September 1948
12.	*K. densiflora*	28	1089	Edith K. Burges	E.A. Bruce	April 1950

*Published in July 1946.
**Rhona Collett (née Brown) (Condy & Rourke 2001).
***Plate later reproduced in Smith et al. (1997).

TABLE 1.—Chronology of southern African, other African, Socotran and Madagascan *Kalanchoe* taxa illustrated in *Flowering Plants of South Africa* and (*The*) *Flowering Plants of Africa* up to 2021 (volume 67). Table updated from Smith et al. (2019). The name under which the species was illustrated, if no longer the one widely used, is given in parentheses in the second column (continued)

#	Taxon of *Kalanchoe*	Volume #	Plate #	Artist	Author(s)	Date
Socotran species						
13.	*K. farinacea*	34	1329	P.R.O. Bally	P.R.O. Bally	March 1960
14.	*K. robusta*	45	1783	Rhona Collett	R.A. Dyer	June 1979
Madagascan species						
15.	*K. tubiflora* (=*Bryophyllum delagoense*)	49	1938	Gill Condy	H.R. Tölken & O.A. Leistner	September 1986
16.	*K. scandens* (=*Bryophyllum beauverdii*)	52	2050	Gill Condy	P.B. Phillipson	May 1992
17.	*K. gastonis-bonnieri*	52	2051	Gill Condy	W. Rauh	May 1992
18.	*K. beharensis*	67	2365	Gill Condy	G.F. Smith, E. Figueiredo & C.C. Walker	June 2021
19.	*K. manginii*	67	2367	Lesley Deysel	G.F. Smith, E. Figueiredo & R. Shtein	June 2021
20.	*K. millotii*	67	2368	Lesley Deysel	G.F. Smith, E. Figueiredo & N.R. Crouch	June 2021
21.	*K. pumila*	67	2369	Lesley Deysel	G.F. Smith & E. Figueiredo	June 2021
22.	*K. serrata*	67	2370	Lesley Deysel	G.F. Smith & E. Figueiredo	June 2021

FIGURE 5.—The leaves of *Kalanchoe pumila* vary from sessile to shortly petiolate and are purplish pink, but covered with a very fine, dusty, white-waxy layer. Photograph: G.F. Smith.

FIGURE 6.—In some forms of *Kalanchoe pumila* the flowers are muted pink to almost white. Photograph: G.F. Smith.

damage from high solar irradiation (Eller & Willi 1977). As the leaves age, the wax coating diminishes through physical action, for example the impact of rain and wind, and also because the leaves expand as they mature with the wax, therefore being spread over a larger surface.

Baker (1883) described *Kalanchoe pumila* based on material collected in central Madagascar by Reverend Richard Baron (1847–1907), an English missionary. Interestingly, in the description, no mention is made of the white, floury wax that so prominently covers virtually all parts of the plant. This likely indicates that Baker had only preserved material at his disposal. Further 'species' described in the 1880s from Madagascar, as *K. brevicaulis* and *K. multiceps*, by Baker (1887) and Baillon (1885) respectively, were synonymised under *K. pumila* when Hamet (1908) produced the first comprehensive treatment of the genus. This view is still followed today. *Kalanchoe pumila* f. *venustior* was described in Boiteau & Allorge-Boiteau (1995) by Boiteau, but this forma, too, is not upheld today.

As implied by the specific epithet 'pumila', derived from the Latin word 'pumilus' which means 'small', *Kalanchoe pumila* was named for its rather small stature. Plants produce comparatively large clusters of seemingly oversized inflorescences with variously shaded pink flowers, for such small plants. The impact of a flowering event seems to be even more severe in *K. pumila* than in *K. blossfeldiana* as store- or nursery-bought plants often wither and die within months after flowering. Should plants of *K. pumila* survive in cultivation for more than one season, they are additionally shy to flower in the outer years. However, with the white, floury coating on its leaves the species remains very striking vegetatively, and it is grown for its foliage as much as for its flowers.

At least up to when it produces flowers for the first time, plants of *Kalanchoe pumila* are easy in cultivation. The species works well as a ground cover in mild, subtropical, or Mediterranean climates (Figure 3) or as a subject to keep in a small container. *Kalanchoe pumila* also grows well in hanging baskets (Figure 8) as in habitat, plants sometimes grow as litho- or epiphytes as well as terrestrially, and obviously prefer well-drained substrates (Rauh 1995). The white, floury coating on the leaves of the plants adds to the charm of the species

FIGURE 7.—The flowers of *Kalanchoe pumila* are most commonly a bright pink colour. The corolla lobes are spreading or strongly recurved and distinctly longitudinally purple-veined. Photograph: G.F. Smith.

in cultivation and should not be deliberately rubbed or washed off.

The species occurs in mountainous parts of the Central Plateau in east-central Madagascar (Boiteau & Allorge-Boiteau 1995; Rauh 1995; Allorge-Boiteau 1996) (Figure 9).

In Afrikaans *Kalanchoe pumila* is commonly known quite aptly as *meelblomplakkie* (for the floury wax covering on the leaves) or as *pienkkalanchoe* (for the flower colour). In English the species is simply known as flower dust kalanchoe, again alluding to the flour dust-like covering on the leaves.

FIGURE 8.—*Kalanchoe pumila* sold as a hanging basket subject in the Garden Shop of the Missouri Botanical Garden, St. Louis, USA. Photograph: G.F. Smith.

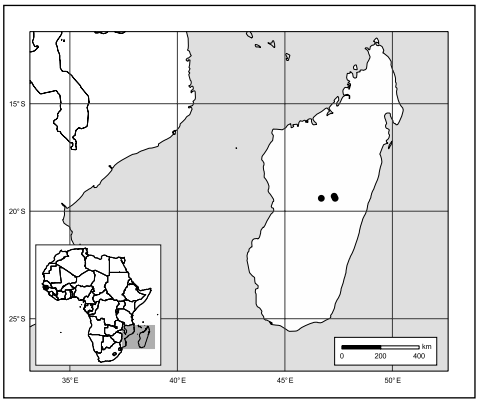

FIGURE 9.—Geographical distribution range of *Kalanchoe pumila* in central Madagascar based on information held in the Global Biodiversity Information Facility and specimens cited in Boiteau & Allorge-Boiteau (1995) that was used for Map 10 reproduced in that work.

Description.—Perennial or short-lived annual, many-leaved, small, branched, glabrous, epiphytic, lithophytic or terrestrial succulent, to 300 mm tall. *Stems* branched, erect to arched to leaning, ± round in cross-section, white-pruinose, raised scars of abscised leaves conspicuous. *Leaves* opposite-decussate, sessile or very shortly petiolate, purplish pink, covered with a very fine, dusty, white-waxy layer, succulent, erect; petiole absent or very short, leaves not clasping the stem; blade 25–45 × 15–25 mm, obovate, flat; base cuneate; apex rounded-obtuse; margins from mid-leaf upwards coarsely crenate or undulate-crenate into rounded, harmless teeth, white-waxy when young, purplish red when older. *Inflorescence* corymbose, short, erect, few-flowered, apically dense, greyish white-waxy; pedicels 6–10 mm long, slender. *Flowers* light to dark violet-pink, longitudinally purple-veined, erect; calyx green to strongly reddish purple-infused; sepals 3–5 × 1.0–2.5 mm, white-pruinose, lanceolate to abruptly triangular, ± separate, basally fused for ± 1 mm, acute-tipped; corolla 6–11 mm long, campanulate to suburceolate; tube 5–10 mm long; lobes 5–10 × 3–4 mm, prominent, spreading to strongly recurved, partly obscuring the corolla tube when recurved, ovate to oblong-ovate, mucronate. *Stamens* inserted well above the middle of the corolla tube, included to slightly exserted, prominently visible at the mouth; filaments short; anthers 0.40–0.75 mm long, reniform, conspicuously yellow. *Pistil* consisting of 4 carpels; carpels 8–11 mm long, light green; styles reddish pink-infused, short; stigmas white, distinctly capitate; scales oblong to rectangular. *Follicles* 9–12 mm long, light green at first, drying greyish brown to black, becoming brittle, grass spikelet-like, enveloped in dry, greyish brown remains of calyx and corolla, apically splitting star-shaped. *Seeds* 0.75–1.00 mm long, light reddish brown to dark brown, cigar-shaped to banana-shaped-curved. *Chromosome number*: $2n = 36$ (Friedmann 1971); $2n = 40$ (Van Voorst & Arends 1982). Plate 2369.

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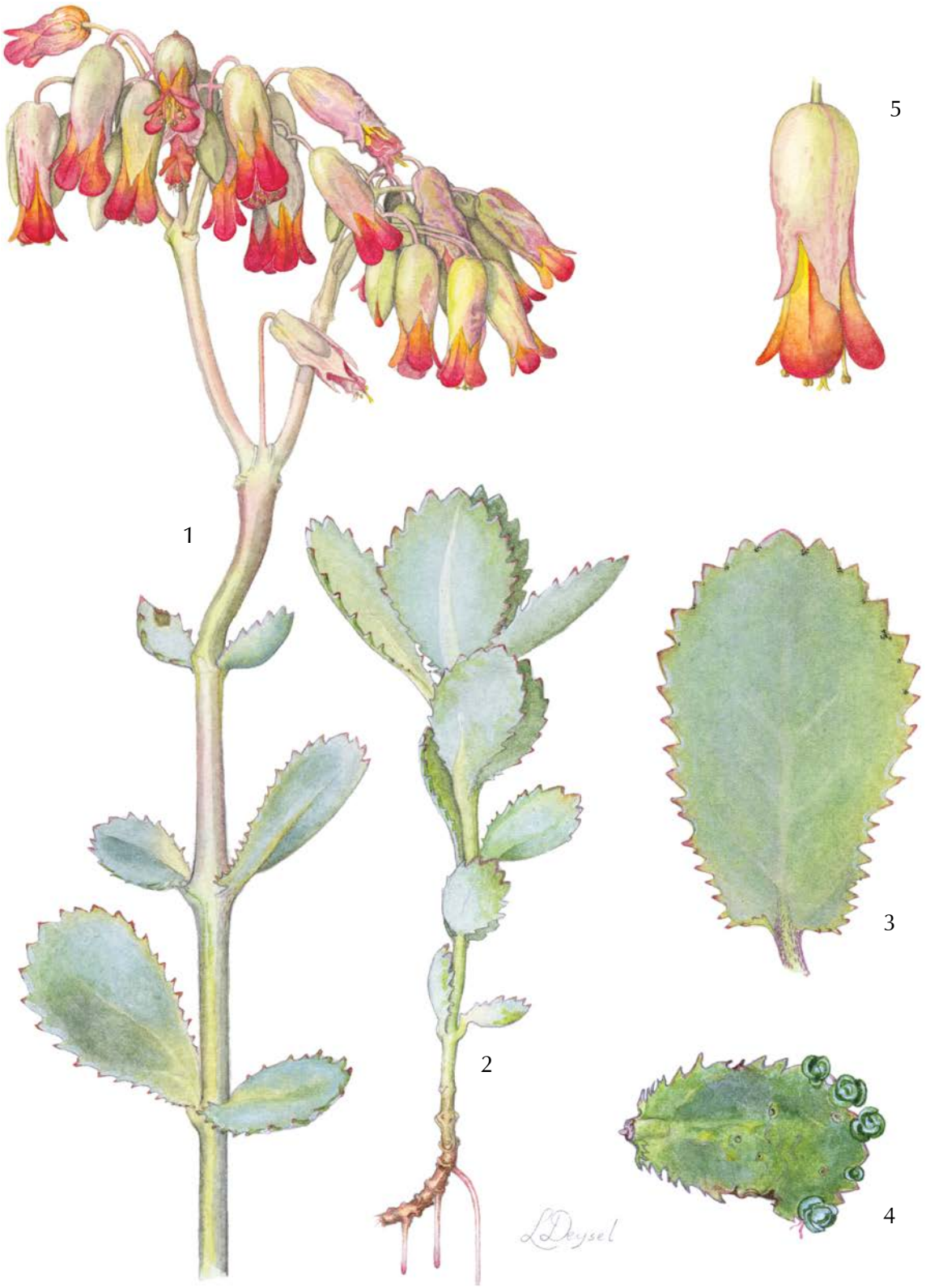

PLATE 2370 *Kalanchoe serrata*

Kalanchoe serrata Crassulaceae: Kalanchooideae

Madagascar

Kalanchoe serrata *Mannoni & Boiteau* in Notul. Syst. (Paris) 13: 152 (1947); Boiteau & Mannoni: 74 (1949); Jacobsen: 289 (1970); Jacobsen: 628 (1986); Boiteau & Allorge-Boiteau: 105 (1995); Rauh: 116 (1995); Descoings: 175 (2003); Smith et al.: 130 (2019a); Smith & Van Wyk: 200 (2019). *Bryophyllum serratum* (Mannoni & Boiteau) Lauz.-March. in Compt. Rend. Hebd. Séances Acad. Sci. 278(20): 2508 (1974) nom. illeg. non Blanco: 220 (1845). *Bryophyllum lauzac-marchaliae* V.V.Byalt in Kaktus Club 1999(3): 27 (1999), as '*luzac-marichaliae*'.

The genus *Kalanchoe* Adans. (Crassulaceae subfam. Kalanchooideae) has its main present-day centre of species diversity in Madagascar, which is often popularly known as l'île Rouge. At least 75 species of *Kalanchoe* are today recognised as occurring naturally on the Red Island, and, in addition, all three subgenera recognised in *Kalanchoe* are represented there. The subgenera are: the autonymic *K.* subg. *Kalanchoe*, *K.* subg. *Bryophyllum* (Salisb.) Koord. and *K.* subg. *Kitchingia* (Baker) Gideon F.Sm. & Figueiredo (Smith & Figueiredo 2018).

About a third of the species of the Madagascan *Kalanchoe* are included in the endemic *K.* subg. *Bryophyllum*. A number of different growth forms have been recorded for these species; one such growth form, broadly referred to as 'shrubby', is common to seven species (Boiteau & Allorge-Boiteau 1995: 16 [page not numbered]; Shtein & Smith 2021). This informal infrageneric group, 'Group VII, Suffrutescentes' (Boiteau & Mannoni 1949), also referred to as '*Kalanchoe* [sect. *Bryophyllum*] subsect. [§. 7] *Suffrutescentes* Boiteau' (Boiteau 1947), includes *K. fedtschenkoi* Raym.-Hamet & H.Perrier (Figure 1), of which especially the variegated-leaved form (Figure 2) is commonly planted in gardens in southern Africa (Smith et al. 2019b).

As is often the case with succulent plant genera that are popular among collectors, their species are frequently burdened by voluminous synonymies as recognition at various taxonomic ranks are accorded to even very minor vegetative or reproductive morphological differences. Such is also the case in *Kalanchoe*, in which a wide variety of diverse growth forms and morphological variability is available to satisfy the curiosity of those who like to hoard these plants. However, perhaps somewhat surprisingly, *K. serrata* (Figure 3) has no heterotypic synonyms. Although the history of the genus dates back to just 10 years after the starting point of modern plant nomenclature (Adanson 1763), *K. serrata* was described only some 75 years ago (Mannoni & Boiteau 1947). Later, when Lauzac-Marchal (1974) argued for the resurrection of *Bryophyllum* as a genus separate from *Kalanchoe*, as earlier published by Salisbury (1805) and later supported by Berger (1930), she transferred *K. serrata* to *Bryophyllum* as *B. serratum* (Mannoni & Boiteau) Lauz.-March. However, this new combination was a later homonym of *Bryophyllum serratum* Blanco, a name that is today

PLATE 2370.—1, inflorescence, × 1; 2, leafy stem, × 0.75; 3, flat leaf showing the adaxial surface, × 1; 4, bulbils forming on the margin of a severed leaf, × 0.75; 5, flower, × 1. Voucher specimen: *G.F. Smith & E. Figueiredo 60* in H.G.W.J. Schweickerdt Herbarium, Pretoria. Artist: Lesley Deysel.

FIGURE 1.—*Kalanchoe fedtschenkoi* has a shrubby growth form similar to that of *K. serrata*, resulting in the two species sometimes being confused. This late-flowering specimen was photographed on 24 November 2017 at the Peak Craft Centre near Piggs Peak in Eswatini (formerly Swaziland). Photograph: G.F. Smith.

included in the synonymy of *K. laciniata* (L.) DC. (Hamet 1908). Later, Byalt (1999), who also preferred recognition of *Bryophyllum* at the rank of genus, published the replacement name *B. lauzac-marchaliae* V.V.Byalt, as '*luzac-marichaliae*', for *B. serratum* (Mannoni & Boiteau) Lauz.-March. Under Article 60.1 of Turland et al. (2018) the epithet is to be corrected to '*lauzac-marchaliae*' as was done in, for example, Descoings (2003). The variable *Kalanchoe laciniata*, a very different species (Blanco 1845), is the type species of *Kalanchoe*.

Like its close relative, *Kalanchoe fedtschenkoi*, *K. serrata* also grows vigorously (Figure 4) in cultivation, and there is always the danger that it will quickly overstay its welcome, with surplus material irresponsibly discarded. This is what has happened in the case of *K. fedtschenkoi*,

FIGURE 2.—The form of *Kalanchoe fedtschenkoi* with white to creamy variegated-leaves is by far the most popular horticultural selection of the species grown in domestic gardens. Photograph: G.F. Smith.

with the species having become naturalised in South Africa at two locations in the southern Cape (Smith & Figueiredo 2017; see Figure 12.20.2 in Smith et al. 2019b). It could also well have been how *K. serrata* came to be recorded for the vascular plant flora of the upper Subachoque River basin in Cundinamarca, Colombia, a region very remote from the natural geographical distribution range of the species in Madagascar (Fernández-Alonso & Hernández-Schmidt 2007). Discarded material of both *K. fedtschenkoi* and *K. serrata* easily strikes root where it is dumped and, in addition, leaves, especially once severed from a plant, develop small, perfectly formed bulbils or plantlets on their margins (Plate 2370, 4). These rapidly sprout roots and shoots, so forming dense colonies. Several kalanchoes, including *K. daigremontiana* Raym.-Hamet & H.Perrier, *K. tubiflora* (Harv.) Raym.-Hamet, and the interspecific hybrid, *K.* ×*houghtonii* D.B.Ward, between these two species, are known to become weedy, even invasive, when allowed to escape from cultivation in places remote from their natural habitats (Smith 2019; Herrando-Moraira et al. 2020). These taxa, especially *K. tubiflora* and *K.* ×*houghtonii*, have been recorded from several places as widely separated as Portugal and Spain (Guillot Ortiz et al. 2009, 2014; Smith et al. 2015; Smith 2019), Florida state in the United States (Ward 2006, 2008) and South Africa (Tölken & Leistner 1986: plate 1938; Smith et al. 2019b).

At first glance, *Kalanchoe serrata* is remarkably similar to *K. fedtschenkoi* in both vegetative and reproductive characters, resulting in the two species often being confused in the literature (see for example Sajeva & Costanzo 2000: 175, where what is labelled as *K. serrata* is likely a form of *K. rosei* Raym.-Hamet & H.Perrier or, less likely, of *K. fedtschenkoi*). The exclusion of *K. serrata* from Raymond-Hamet &

FIGURE 3.—Plants of *Kalanchoe serrata* are medium-sized shrubs with light green to glaucous green leaves that are often flexed into one direction. Photograph: G.F. Smith.

FIGURE 4.—In cultivation *Kalanchoe serrata* will soon form large clumps of multi-branched stems. Photograph: G.F. Smith.

FIGURE 5.—The brownish green stems of *Kalanchoe serrata* develop masses of stilt-like roots. Photograph: G.F. Smith.

Marnier-Lapostolle (1964) may even have been tacit rejection of *K. serrata* as a 'good' species as the name was published more than 15 years earlier, and Raymond-Hamet, the global expert on the genus in the mid-20th century (Smith 2020), certainly had knowledge of Mannoni & Boiteau (1947).

However, *Kalanchoe fedtschenkoi* and *K. serrata* can be separated on several characters (Table 1). Like *K. fedtschenkoi*, *K. serrata* is a perennial, low-growing to medium-sized, succulent shrub that consists of numerous erect to variously leaning branches that root where they touch the ground. The stems also root by means of thin, but tough, stilt-like roots that variously develop low down or high up on branches (Figure 5). The leaves of *K. serrata* are basally slightly winged (Figure 6, left), while those of *K. fedtschenkoi* are cuneate (Figure 6, middle). The leaf margins of *K. fedtschenkoi* are irregularly crenate, with fairly large, rounded crenations. In contrast, the leaves of *K. serrata* are serrate-dentate with sharp-tipped, but harmless, teeth (Figure 7), and the leaves tend to be rather flat at maturity, but soup plate-like turned up along the margins when young. Flower colour of *K. serrata* varies from reddish to yellowish (Figure 8, right). However, the flowers of *K. fedtschenkoi* are consistently orange to pinkish orange (Figure 8, left). In both species the flowers are carried in apically branched, rather flat-topped inflorescences. At least in some forms of *K. serrata* the flowers

FIGURE 6.—The leaves of *Kalanchoe serrata* (left) are basally slightly winged to slightly to distinctly auriculate. At maturity, leaves of *K. fedtschenkoi* are mostly basally cuneate (centre and right). A leaf of the variegated form of *K. fedtschenkoi* is shown on the right. Photograph: G.F. Smith.

FIGURE 7.—The leaves of *Kalanchoe serrata* have smooth surfaces and the leaf margins are toothed with fine saw tooth-like serrations, virtually for their entire length. Photograph: G.F. Smith.

TABLE 1.—Vegetative and reproductive characters on which *Kalanchoe serrata* can be distinguished from *K. fedtschenkoi*

Character	***Kalanchoe serrata***	***Kalanchoe fedtschenkoi***
Leaf shape	Ovate	Obovate, oblong or round
Leaf venation	Often conspicuous	Hardly visible
Leaf base	Slightly auriculate; auricles not flared	Cuneate
Leaf margins	± Soup plate-like curved upwards along the margins when young, rather flat at maturity	± Flat
Leaf marginal crenations	Along entire margin	Especially in the upper half
Disposition of flowers post-anthesis	± Suberect	Pendulous
Flower colour	Red, reddish purple, pinkish, orange, to pale yellow	Orange to pinkish orange

FIGURE 8.—Flower colour of *Kalanchoe serrata* varies from reddish to yellowish (right). The flowers of *K. fedtschenkoi* are consistently orange to pinkish orange (left). Photograph: G.F. Smith.

FIGURE 9.—Flowers of *Kalanchoe serrata* are pendulous but often slightly horizontally flared, becoming suberect when dry. Photograph: G.F. Smith.

have a tendency to be slightly horizontally flared, becoming suberect to erect when dry (Figure 9).

Like the vast majority of species of *Kalanchoe*, *K. serrata* flowers in winter and early spring, in the southern hemisphere, from June to September, with a peak from July to August.

In South Africa *Kalanchoe serrata* is known as *tandkalanchoe* or *tandplakkie* in Afrikaans, and as saw tooth kalanchoe in English, with, in both instances, reference being made to the small teeth along the leaf margins. The same character is of course also referenced in the specific epithet, *serrata*.

Kalanchoe serrata is indigenous to east-central Madagascar (Figure 10).

Description.—Perennial, erect to spreading, tuft-like, glabrous, brittle shrubs, densely branched especially from the base, with haphazard, untidy canopies; succulent, to 0.5(–0.6) m tall, annually increasing in size. *Stems* thin, light green when young, becoming brown, variously erect, leaning or prostrate (creeping), rooting along the way, erect and leaning branches developing long, near-woody stilt-like roots; bark slightly peeling to flaking with age, hard, brown. *Leaves* many, very densely packed in young plants, more widely dispersed on older stems, erect to variously slanted away from branches, often in one plane, succulent, glabrous, petiolate, flattened above and below, often slightly indented above and below along midrib and leaf veins, green to glaucous green, slightly waxy, wax easily rubs off; petiole robust, light whitish green, succulent, 1–25 mm long; blade 20–60 × 15–30 mm, ovate, succulent; base winged to slightly to distinctly auriculate; apex rounded-obtuse; margins irregularly toothed with well-defined, round-tipped or acute crenations along entire length of margin, depressions between teeth usually dark brown purple, crenations somewhat angled towards apex, forming bulbils (adventitious buds) in the depressions between crenations especially once leaves are detached. *Inflorescence* a terminal, apically branched, many-flowered head-shaped corymb, 200–300 mm tall, erect;

some corymb branches terminating in sterile, curved, pedicel-like branchlets; peduncle straight, light brownish purple; pedicels 6–15 mm long, glabrous. *Flowers* 4-merous, pendent, becoming suberect when dry, glabrous, subtended by small leaf-like bracts that remain persistent for a long time, waxy bloom absent, papery when dry, dries a deeper shade of purple than calyx; calyx tubular for ± two-thirds; sepals 12–18 mm long, free portion elongated-triangular, fused for ± 8–15 mm, acute, obscuring up to three-quarters of the corolla tube, light greenish to light greenish purple, purple more prominent along centre of sepal, purple arranged in faint to distinct longitudinal lines; corolla red, reddish purple, pinkish, orange, to pale yellow, yellowish where covered by calyx, longitudinally infused with pinkish red in centre and along margins of petal; tube 12–20 mm long, cylindrical, slightly flared at the mouth; lobes ± 6 × 4 mm, obovate, apically obtuse. *Stamens* inserted very low down in corolla tube at ± upper end of carpels, slightly exserted; filaments ± 15 mm long, thin, purplish red; anthers ± 0.5–1.0 mm long, black, slightly exserted; pollen yellowish grey to dark grey. *Pistil* consisting of 4 carpels; carpels 6–7 mm long, light shiny green; styles 15–18 mm long; stigmas very slightly capitate, green, later slightly exserted; nectary scales ± square, free, ± 1 × 1 mm, shiny light yellowish green, slightly indented above. *Follicles* 5–7 mm long, enveloped in purple to purplish light brown, papery remains of calyx and corolla, slowly splitting lengthwise when dry. *Seeds* 0.40–0.75 mm long, dark brown to blackish brown, cylindrical, not club-shaped to slightly banana-shape-curved. *Chromosome number*: unknown. Plate 2370.

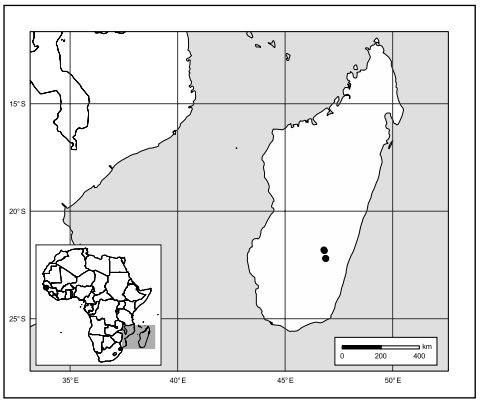

FIGURE 10.—Geographical distribution range of *Kalanchoe serrata* in Madagascar based on information held in the Global Biodiversity Information Facility and specimens cited in Boiteau & Allorge-Boiteau (1995: 105–106) that was used for Map 10 [p. 200, page not numbered] reproduced in that work.

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Bersama lucens Melianthaceae

Eswatini, Mozambique, South Africa

Bersama lucens *(Hochst.) Szyszył.* in Polypetalae Disciflorae Rehmannianae 2: 50 (1888); Phillips: 37 (1921); Verdcourt: 244 (1950); White: 547 (1966). *Natalia lucens* Hochst. in Flora 24: 663 (1841); Sonder: 369 (1859–1860).

Bersama lucens, popularly known as glossy bersama or glossy white-ash, was described by Szyszyłowicz as 'a very distinct species from South Africa with obovate, obtuse, cuneate leaflets which have distinctly different venation. Leaves 1–3-jugate only. Fruit rugose. Stigma not capitate. Disc two-lobed' (Verdcourt 1950). The genus name was derived from *brsma*, a name used for the genus in Ethiopia (Quattrocchi 2016) where the prominent *B. abyssinica* Fresen., together with *Ritchiea albersii* Gilg, ranked as the most scarce medicinal plants in the Meinit District (Giday et al. 2009). The Latin species name refers to the shiny leaves, notably the young leaves (Quattrocchi 2016). Other vernacular names for *B. lucens* in South Africa are *blinkblaarwitessenhout* (Afrikaans), *undiyaza* (isiZulu) and *isindiyandiya* (isiZulu and isiXhosa). The isiZulu and isiXhosa names for *B. lucens* have also been used for other species in the genus like *B. swinnyi* E.Phillips and *B. tysoniana* Oliv. (Hutchings et al. 1996; Boon 2010).

Bersama lucens is a member of the relatively small family Melianthaceae Horan., which consists of four genera namely *Bersama* Fresen. (eight species), *Greyia* Hook. & Harv. (three species) and *Melianthus* L. (six species), all with distribution ranges in Africa; and *Francoa* Cav. (three species) in South America (The Plant List 2020). *Bersama stayneri* E.Phillips is considered a synonym of *B. tysoniana* (African Plants Database 2020). *Greyia* and *Francoa* were previously placed in Greyiaceae and Francoaceae respectively. Due to similarities in certain traits, the families were merged with the Melianthaceae (APGII 2003). Prior to Melianthaceae being accepted as a family in 1891, there were opposing views on the placement of *Bersama* and *Melianthus*, in either the Rutaceae or Sapindaceae (Doweld 2001). In 1831 Johann Heinrich Friedrich Link (1767–1851), a German naturalist from Berlin, recognised the Melianthaceae as described by Paul Fedorowitsch Horaninow, a Russian botanist (Gledhill 2008; Stubbendieck el al. 2017). About two decades later, Jules Èmile Planchon (1823–1888), a French botanist and past director at the Botanical Garden of Montpellier (Balfour et al. 1888–1889), proposed a new natural order, Meliantheae, with two sections and four genera. He recognised the genera *Bersama*, *Diplerisma* J.E. Planch., *Melianthus* and *Natalia* Hochst., each with two species. Planchon disputed the newly proposed order's relationship to the Rutaceae and the Zygophylleae, and described characters for the Meliantheae as being closely allied to Sapindaceae and Geraniaceae (Planchon 1851). The Zygophylleae was the first section in Jussieu's Rutaceae which Robert Brown (1814) recognised as a distinct taxon, now the Zygophyllaceae (bean-caper family) with 26 genera and 211 species. Sonder's (1859–1860) classification of the order Meliantheae was similar to Planchon's

PLATE 2371.—1, inflorescence, × 1; 2, fruiting twig, × 1. Voucher specimen: *Condy 245*, in National Herbarium, Pretoria. Artist: Gillian Condy.

PLATE 2371 *Bersama lucens*

(1851), however he recognised two tribes, each with one genus namely *Melianthus* (four species) and *Natalia* (one species), and placed *Diplerisma* in synonymy with *Melianthus*. He referred to *Melianthus dregeanus* Sond. as a remarkable species with capsules approaching that of *Bersama* and *Natalia*. More recently, Doweld (2001) reported that differences in fruit and seed morphology, and anatomical characters of *Bersama* and *Melianthus* supported the placement of *Bersama* in a distinct family, Bersamaceae Doweld. Soon thereafter, the Bersamaceae was placed in synonymy with the Melianthaceae (APGII 2003).

The genus *Bersama* was described in 1837 by Fresenius in *Museum Senckenbergianum* (Schmidt 1998). He grouped plants with five stamens, a five-loculed superior ovary, filiform style, and a five-lobed stigma with thick, erect lobes into *Bersama* (Fresenius 1837). Shortly thereafter, Hochstetter (1841) described the monotypic genus, *Natalia*, in *Flora*. Hochstetter's description of *Natalia lucens* was based on a plant collected by Ferdinand Krauss. Krauss made a voyage to South Africa from 1838 to 1840 during which time he collected the new species on the edge of the woods near the Umlass [Umlaas] River in Natal (now KwaZulu-Natal), as recorded on specimens kept at the Missouri Botanical Garden Herbarium (MO). Plants with four stamens, a four-loculed ovary, glabrous style, and an obtuse, subtetragonous stigma were placed in *Natalia* (Baker 1907) and these characters separated it from *Bersama*. Wood and Evans (1899) pointed out that the difference between the genera was that only two stamens in *Natalia* are connate, while in *Bersama* all stamens are connate. In 1907, Edmund Gilbert Baker explained that his father's (John Gilbert Baker) arrangement (Baker 1868) was to place plants with four stamens in Section *Natalia* and those with five stamens in Section *Eubersama*. Gürke (1895) made similar groupings. The younger Baker also observed that stamens in some *Bersama* species vary in number, either four or five (even in flowers on the same raceme), leading him to combine the sections in his treatment. Therefore, in 1907 Baker published *B. lucens* in *The Journal of Botany* and listed *Natalia lucens* Hochst. as a synonym.

Bersama occurs in southern and tropical Africa. In the Flora of southern Africa region (South Africa, Eswatini, Lesotho, Botswana and Namibia) three species are recognised, namely *B. lucens*, *B. swinnyi* and *B. tysoniana* (including *B. stayneri* as a synonym) (BODATSA 2020). The latter two species are endemic to southern Africa. Four more species, namely *B. abyssinica*, *B. palustris* L.Touss., *B. swynnertonii* Baker f. and *B. yangambiensis* L.Touss., occur in tropical Africa, in Cameroon, the Democratic Republic of the Congo (DRC), Kenya, Zimbabwe, Tanzania and Uganda (Verdcourt 1950; Quattrocchi 2016). *Bersama abyssinica* has three subspecies, namely *B. abyssinica* subsp. *abyssinica*, *B. abyssinica* subsp. *paullinioides* (Planch.) Verdc. and *B. abyssinica* subsp. *rosea* (Hoyle) Mikkelsen (The Plant List 2020). *Bersama abyssinica* subsp. *paullinioides* was considered a synonym of *B. abyssinica* subsp. *abyssinica* by Mikkelsen & Seberg (2001). *Bersama*, though a small genus, presents a range of taxonomic uncertainties and changes in circumscription, suggesting the need for a taxonomic re-evaluation. Table 1 compares morphological and distribution characters of *Bersama* species. Early taxonomic treatments on *Bersama* (Gürke 1895; Brehmer 1917) were published mainly for tropical African species. The first treatment of *Bersama* in South Africa was presented by Phillips (1921) in the first volume of the journal *Bothalia*. White (1966) presented a treatment of the Melianthaceae for the Flora Zambesiaca region where he recognised one genus, *Bersama*, with three species, namely *B. abyssinica*, *B. swynnertonii* and *B. lucens*. He noted that these species were distinct in

TABLE 1.—A comparison of the morphology and distribution of *Bersama* species; from Phillips (1921); Verdcourt (1958); Toussaint (1959); White (1966); Coates Palgrave (2002); Boon (2010); African Plants Database (2020)

Species	**Leaflets**			**Inflorescence**		**Petals**		**Fruit**	**Distribution**
	Arrangement	Size (mm)	Margins	Arrangement	Length (mm)	Colour	Length (mm)	Capsules	
B. abyssinica	4–6 pairs of opposite leaflets plus the terminal one	35–220 × 10–80	Entire or deeply toothed	Spike-like racemes	± 350	Greenish to creamy yellow tinged with purple	20	Spherical, not warty	DRC, Malawi, Mozambique, Tanzania, Zimbabwe
B. lucens	1–3 pairs of opposite leaflets plus the terminal one	20–95 × 10–45	Entire, wavy (immature leaves serrate)	Racemes	± 150	Greenish white to dull yellow	6	Spherical, hairy	Eswatini, Mozambique (marginal), South Africa (Eastern Cape, KwaZulu-Natal, Mpumalanga)
B. palustris	6–8 pairs of opposite leaflets plus the terminal one	50–120 × 18–40	Serrate	Racemes	–	–	30	Hairy	DRC
B. swinnyi	4–7 pairs of opposite leaflets plus the terminal one	20–80 × 9–35	Entire (immature leaves serrate)	Axillary racemes	± 50	Greenish white	13	Spherical, very warty	South Africa (Eastern Cape, KwaZulu-Natal)
B. swynnertonii	2–4 pairs of opposite leaflets plus the terminal one	80 × 35	Entire	Upright racemes	± 180	Purplish red	18	Spherical, hairless	Mozambique, Zimbabwe
B. tysoniana (including *B. stayneri*)	4–6 pairs of opposite leaflets plus the terminal one	15–90 × 7–40	Entire or serrate in upper half	Terminal racemes	± 170	Greenish white to cream	11–15	Spherical, warty or wrinkled	Eswatini, South Africa (Eastern Cape, KwaZulu-Natal, Limpopo, Mpumalanga)
B. yangambiensis	4–7 pairs of opposite leaflets plus the terminal one	130–280 × 45–85	–	Axillary racemes	± 400	Greenish white	20	Pear-shaped	DRC

the region, including in South Africa, unlike the tropical species, especially *B. abyssinica*, which are 'excessively variable and difficult to classify' (White 1966). Verdcourt, presented a quartet of treatments on *Bersama* between 1950 and 1989. His view was that the genus' taxonomy was in chaos due to the large number of species and infraspecific taxa published since 1937, which arose mainly because authors failed to recognise that some species are exceptionally polymorphic (Verdcourt 1950; Beentje et al. 2013). Previously, descriptions of new species were often based on a single specimen or incomplete material with obscure characters. In addition, many of the type specimens that were selected by Brehmer (1917) and Gürke (1895) were destroyed during World War II, leaving a gap in reference collections for interpreting descriptions. Verdcourt (1950) attempted to address the confusion in the genus and described eight varieties for *B. abyssinica*, which Mikkelsen & Seberg (2001) subsequently sunk under two subspecies, *B. abyssinica* subsp. *abyssinica* and *B. abyssinica* subsp. *rosea* (Hoyle) Mikkelsen. The number of synonyms listed under *B. abyssinica* subsp. *abyssinica* in Mikkelsen and Seberg (2001) demonstrates the connection in *Bersama* between polymorphism and number of descriptions of new species; sterile specimens cannot be determined with absolute certainty.

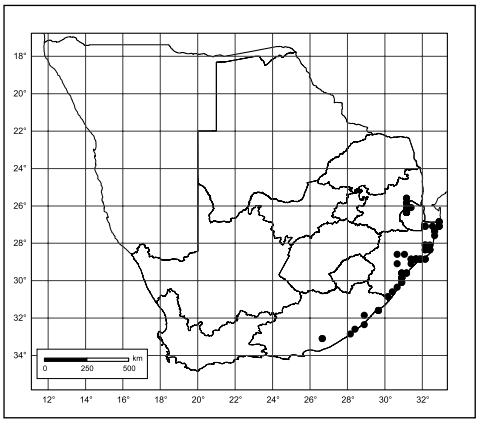

FIGURE 1.—Known geographical distribution of *Bersama lucens* in southern Africa.

According to records in the Botanical Database of Southern Africa (BODATSA), *Bersama lucens* was collected as early as November 1830 by Drège from Hermanuskraal between the Fish River and Fort Beaufort, Eastern Cape (*Drège s.n. PRE0593306* and *Drège s.n. PRE0273695*, both in PRE). This was followed by a collection by John Medley Wood in September 1886 from the Durban flats near Umgeni, KwaZulu-Natal (*J.M. Wood s.n. NH0002868* in NH).

In southern Africa, *Bersama lucens* is found at altitudes ranging from close to sea level to about 1 530 m above sea level and it occurs in a number of habitats, including forests, forest margins, bushveld, kloofs, thickets and coastal dunes, often in rocky areas (Moll 1981; Van Wyk & Van Wyk 1997; Joffe 2001). *Bersama lucens* occurs in the eastern regions of South Africa from Hermanuskraal near Makhanda [Grahamstown] in the Eastern Cape (Drège's specimen) northwards mostly along the coast of KwaZulu-Natal to Lake Sibaya. It also extends into Mbombela [Nelspruit] in Mpumalanga, Eswatini and to the extreme south of Mozambique (Figure 1) (BODATSA 2020).

Bersama species are widely used in traditional remedies in Africa. In West Africa, decoctions of the bark, leaf or root from *B. abyssinica* subsp. *paullinioides* are consumed as a laxative for stomach disorders such as abdominal pain, colic, diarrhoea, cholera, intestinal worms, amoebiasis, dysentery, as well as rabies, malaria and sexually transmitted diseases (Zekeya et al. 2014). In Cameroon, *B. abyssinica* is used to treat rheumatism and snake

bites, and used as an aphrodisiac (Zekeya et al. 2014). The species is also used in treating cancer, convulsions and tonsillitis (Neuwinger 2000; Giday et al. 2009; Zekeya et al. 2014). In this regard, a study by Vanhaelen et al. (1972) shows that *B. yangambiensis* has cardiotonic and antitumour properties.

A century ago senior forest research officer, Colin Robertson, initiated studies into the medicinal properties of *Bersama* species in southern Africa. Mr Robertson examined the bark of *B. swinnyi* and *B. tysoniana* and found they have either a bitter, or a bitter and burning taste. This characteristic seemed to be an indicator of their medicinal value (Phillips 1921). The bark of *B. lucens*, *B. swinnyi* and *B. tysoniana* is reportedly used to treat menstrual pain, infertility, impotency and leprosy (Watt & Breyer-Brandwijk 1962; Hutchings et al. 1996). *Bersama lucens* is furthermore also used for nervous system disorders, mental disorders and headaches, and shown to be effective in laboratory trials by relieving spasms in the small intestine of guinea pigs. The roots and leaves of *B. lucens*, however, have reportedly been linked to fatalities in KwaZulu-Natal (Watt & Breyer-Brandwijk 1962; Hutchings et al. 1996; Neuwinger 2000; Boon 2010). *Bersama lucens* has been used as a charm protector to ward off evil, for protection against lightning strikes and to cause confusion against rivalries in court (Hutchings et al. 1996). Maroyi (2020) documented the major medicinal uses of *B. lucens* in southern Africa and cautioned that, since toxic heart glycosides were extracted from the closely related *B. abyssinica*, the medicinal use of *B. lucens* should include rigorous toxicity screening of plant parts. Besides their medicinal value, *Bersama* species are also used for firewood, poles, insecticides and to produce furniture (Coates Palgrave 2002; Lemmens 2020).

Bersama species are beautiful shrubs or trees with dense foliage, striking new leaves and woody, knobbly capsules (Pooley 1993). *Bersama lucens* makes for an attractive garden plant with its glossy, brownish purple new foliage (Van Wyk & Van Wyk 1997). Joffe (2001) explains that cultivation of *B. lucens* can easily be achieved through seed germination. Carr (1994) attempted to grow three species, *B. abyssinica*, *B. lucens* and *B. tysoniana*, from seed and found seeds of *B. lucens* collected in KwaZulu-Natal, but propagated in the Highveld region, failed to germinate. The species thrives in nutrient-rich, well-drained soil that contains adequate amounts of water and compost. The tree grows best in warm areas and makes for an excellent shrub border or background plant, most suitable in urban gardens and parks (Joffe 2001).

The flowers of *Bersama* are small, greenish white, with narrow stalks and long, narrow tubes, and attract butterflies (Pooley 1993; Joffe 2001; Boon 2010). Larvae of the Common Hairtail butterfly, *Anthene definita* (Family: Lycaenidae) (Palmer & Pitman 1972; Pooley 1993; Joffe 2001), and the Silver-barred Emperor, *Charaxes druceanus* (Family: Nymphalidae) (Van Somersen & Rogers 1928), have been recorded to feed on the leaves of *B. abyssinica* and *B. lucens* (Boon 2010). More observations of caterpillar interaction with *Bersama* are required as some records of *Bersama* as larval hostplants may be erroneous (Larsen 1991; Williams 2018).

Flowering and fruiting times of *Bersama lucens* overlap. Plants start flowering from September and some individuals may flower as late as June. Fruits usually develop from

FIGURE 2.—*Bersama lucens*: a, inflorescences; b, close-up of flowers; c, fruit; d, close-up showing shiny (lucent) upper surface of leaves. Photographs: a–c, G. Nichols; d, E. Moll.

February to August. The capsules split into three or four valves to display the striking bright red seeds with yellow arils at their bases (Figure 2). These conspicuous displays attract vervet monkeys and birds (Joffe 2001; Quattrocchi 2016).

Description.—Perennial shrub or small to medium-sized tree, 1.5–9.0 m high. *Main stem* single or multi-stemmed. *Bark* pale grey to brown, rough, with long crevices with small cracks; wrinkled on branchlets. *Leaves* pinnately compound, 40–75 × 25–45 mm, 1–3 pairs of alternate leaflets plus a terminal one; leaflets obovate to oblong, glabrous, leathery and thick, dark green, purplish to reddish brown on new growth; margin thickened, wavy, entire; base cuneate; apex rounded; venation pronounced, midrib and lateral veins yellow; petiolules short; petiole 20–25 mm long. *Flowers* in racemes, up to 150 mm long; buds small, oval; pedicels slender, 6.0–8.5 mm long. *Calyx* olive-green, hairy, 4 × 2 mm. *Corolla* greenish cream, white or dull yellow; petals 5, narrowly oblong, ± 6 × 2.5 mm. *Stamens* 4; anthers 2-celled, ovoid, 2.5 × 1.5 mm; filaments all connate at base, terete, 1 mm long. *Ovary* subglobose, densely villous, 1 × 1.5 mm, 4-loculed with 1 ovule per locule; stigma minute, spherical, slightly lobed; style filiform, cylindrical, 7 mm long. *Capsule* subglobose, large, ± 20 mm in diameter, velvety brown, woody, wrinkled, splits into 3 or 4 valves. *Seeds* bright red, partially covered by yellow, fleshy, cup-shaped aril, 9 × 6 mm. *Flowering time*: September to June and collected in fruit from February to August. Plate 2371.

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Argomuellera macrophylla Euphorbiaceae

Tropical Africa

Argomuellera macrophylla *Pax* in Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 19: 90 (1894); Radcliffe-Smith: 225 (1987); Radcliffe-Smith: 147 (1996); White et al.: 242 (2001); Coates Palgrave: 504 (2002); Van Wyk & Van Wyk: 162 (2013); Burrows et al.: 433 (2018). *Pycnocoma laurentii* De Wild.: 285 (1908). *Pycnocoma sapinii* De Wild: 285 (1908). *Pycnocoma hirsuta* Prain: 51 (1909). *Pycnocoma parviflora* Pax: 81 (1909). *Wetriaria macrophylla* (Pax) Pax: 50 (1914).

Argomuellera Pax, a small genus in the Euphorbiaceae, is fairly common in tropical evergreen lowland and submontane African forests (Webster 1994; White et al. 2001). The genus consists of about 12 species of which six are restricted to Madagascar and the Comoro Islands, with the rest occurring in other regions of Africa (Radcliffe-Smith 1996; McPherson 2012). The genus belongs to the tribe Pycnocomeae of the subfamily Acalyphoideae (Radcliffe-Smith 2001; McPherson 2012). According to Kenfack et al. (2015), sterile members of *Argomuellera* are often confused with members of the genera *Pycnocoma* Benth. and *Crotonogynopsis* Pax, and also with members of the Violaceae, namely *Rinorea ferruginea* Engl. and members of the genus *Allexis* Pierre (Van Wyk & Van Wyk 2013). It can, however, be distinguished from the related genera *Pycnocoma* and *Droceloncia* J.Léonard mainly by features of its pistillate flowers, which differ in being borne laterally on the inflorescence and in possessing a disc (McPherson 2012).

The genus was named in honour of Swiss professor of botany, Jean (Johannes) Mueller, called Argoviensis (Aargau or Argovie, Switzerland), whose work was one of the first on the classification of the family Euphorbiaceae (Webster 1994; Quattrocchi 1999). Mueller was the owner of a lichenological herbarium, curator of the Candolle and B. Delessert herbaria, and the director of the Geneva Botanic Garden, all during the 1800s (Quattrocchi 1999). The specific epithet is derived from the Greek words *makros*, meaning 'long', and *phyllon*, meaning 'leaf', alluding to the size of the species' leaves (Burrows et al. 2018). Common names of the species include undershrub bigleaf and *onderbosgrootblaar* (Afrikaans) (Burrows et al. 2018).

The first description of the species was provided by Pax (1894) who relied on specimens collected by various collectors. From Pax's list of cited specimens, the first ever specimen to be collected was by Pogge from the Congo area on 1 June 1883. The species is widespread in tropical Africa (Figure 1), from Equatorial Guinea to the Congolian rain forests, eastwards of Sierra Leone and further east to Ethiopia and southwards to Angola, Zambia, Zimbabwe and Mozambique (White et al. 2001). The species occurs in diverse forest areas (evergreen rain and mist forests). In West Africa it grows in drier kinds of forests,

PLATE 2372.—1, flowering branch, × 1; 2, flower showing recurved sepal lobes and numerous yellowish stamens, × 2; 3, three-lobed ovary with triangular-ovate sepals enclosing ovary and three stigmatic lobes at top, × 1; 4, fruiting branch, × 2. Voucher specimen: *Condy 283* in National Herbarium, Pretoria. Artist: Gillian Condy.

PLATE 2372 *Argomuellera macrophylla*

whilst in East Africa it is frequent in riverine forests and evergreen lakeshore forests at altitudes of 1 300–1 850 m above sea level (Radcliffe-Smith 1996; Schmelzer 2007). *Argomuellera macrophylla* flowers from September and fruits appear towards the end of March (Van Wyk & Van Wyk 2013). The southernmost distribution of this species was recorded in Zimbabwe, Manicaland, in the Chirinda Forests bordering Mozambique.

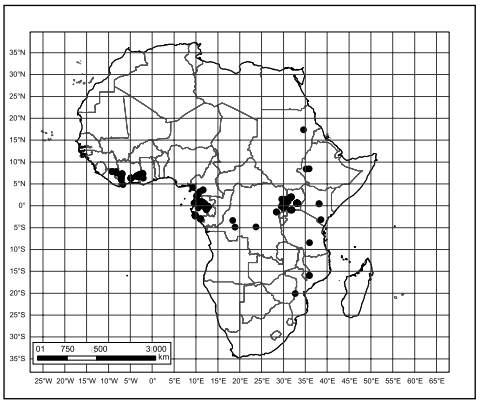

FIGURE 1.—Known distribution of *Argomuellera macrophylla* in tropical Africa based on collection data from the Global Biodiversity Information Facility (2020) and Pretoria National Herbarium (PRE).

Argomuellera macrophylla is characterised by elliptic-oblanceolate leaves with coarsely serrate margins. According to Radcliffe-Smith (1975), it is closely related to *A. basicordata* Peter ex Radcl.-Sm., but can be distinguished by its margins that are sharply and coarsely serrate (Figure 2a) and attenuate to acute bases, whereas *A. basicordata* has margins that are subentire and narrowly rounded or cordate bases. The cymose inflorescence bears several actinomorphic, unisexual flowers. After anthesis, the male flowers exhibit numerous free stamens, with filaments as long as the pedicels, and produce copious amounts of aperturate pollen (Figure 3a). Anthers have an attractive pale yellow colour. The trilobate, hairy fruits (Figure 2b) are attached on short pedicels or are sometimes subsessile (Radcliffe-Smith 1987). The outer surface of calyx and fruits are pubescent with sharp eglandular hairs (Figure 3b). With its large leaves and fluffy racemes, *A. macrophylla* is often confused and associated with *Rinorea ferruginea* (Van Wyk & Van Wyk 2013). Examination of material at PRE indicates that *A. macrophylla* is potentially polymorphic over its wide distribution range of forest types and ecological conditions, and therefore warrants further investigation to gain clarity on intraspecific variation within the species.

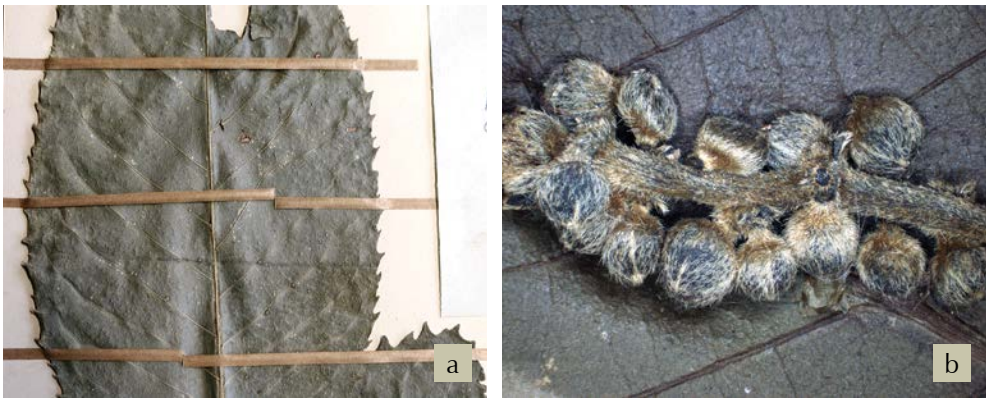

FIGURE 2.—Herbarium specimens of *Argomuellera macrophylla*: a, margin sharply serrate; b, hirsute fruit. Voucher specimens: a, *Rattray 1164* (PRE); b, *Van Wyk BSA 1212* (PRE). Photographs: M. Maswoliedza.

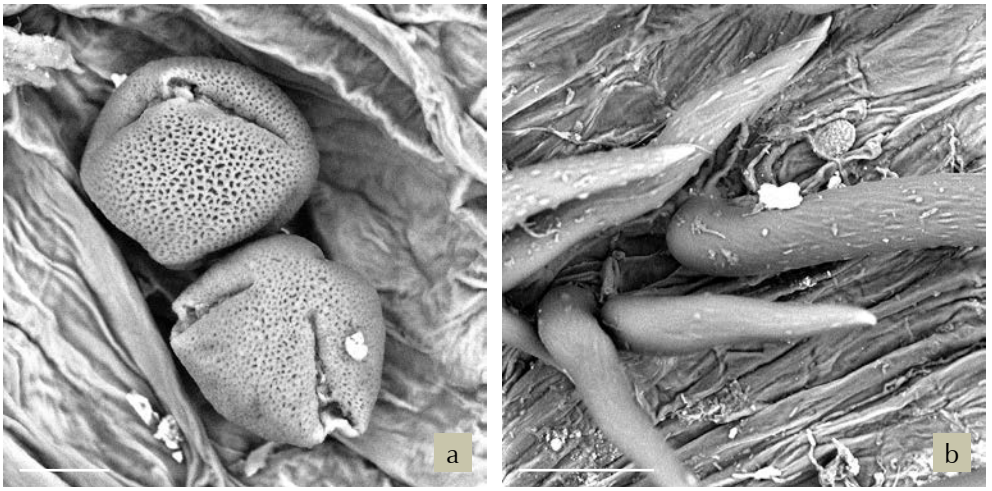

FIGURE 3.—Scanning electron micrographs of *Argomuellera macrophylla*: a, pollen grains showing apertures; b, outer surface of calyx showing sharp eglandular hairs. Scale bars: a, 10 μm; b, 30 μm. Voucher specimen: *Van Wyk BSA 1212* (PRE). Photographs: a, b, R.J. Sebola & M. Maswoliedza.

No nectaries have been reported in *Argomuellera macrophylla* and pollination syndromes remain speculative. Pollen could possibly be the reward for potential pollinators. However, the arrangement of staminate flowers along the inflorescence axis, coupled with the radial display of the stamens upon anthesis, suggest that wind could be a major mechanism by which *A. macrophylla* achieves pollination. There is the possibility for self-pollen (inter- and intra-inflorescence) to land on pistillate flowers due to gravity and the indiscriminate nature of wind pollination. Whether there is self-compatibility or incompatibility within *A. macrophylla* remains to be tested. The older pistillate flowers appear to be at the base of the inflorescence, and therefore most likely to open and mature first. At maturity, the capsules in *A. macrophylla* open through explosion along the sutures, thus facilitating the dispersal of seeds.

The leaf sap is used as a purgative and emetic in the treatment of poisonings and for ascites, whereas the powdered dry leaves can sometimes be used as an aphrodisiac (Burkill 1994). According to Schmelzer (2007), little is known about the phytochemistry of the species and it is likely to remain utilised for what it is currently known for by local people. The nectar from the flowers is thought to be poisonous (Schmelzer 2007).

Description (after Radcliffe-Smith (1996), Van Wyk & Van Wyk (2013), and based on specimens in PRE).—A slender evergreen unbranched or sparingly branched shrub or small tree, up to 9 m high. *Stems* with bark ± smooth; young shoots and petioles pubescent, later glabrescent. *Leaves* oblanceolate, rarely broadly ovate; apices acutely acuminate; bases attenuate to acute; 140–250 × 45–116 mm; upper surface glabrescent or glabrous; undersurface hirsute with spreading hairs; margins serrate; midrib and main nerves hirsute pubescent abaxially, bright red when young; petiole hardly defined due to downward extending leaf base. *Stipules* up to 15 mm long, linear, pubescent. *Inflorescence* up to 200 mm long, with peduncles 22 mm long, axis densely or evenly pubescent; bracts

2 mm long, spreading, triangular-ovate. *Flowers* sweetly scented. *Male flowers*: pedicels up to 5 mm long; calyx lobes 2–4 × 4–5 mm, becoming reflexed, ovate to lanceolate, densely appressed pubescent outward, glabrous inward, white; disc glands numerous, bright orange; stamens 30–40, 4–7 mm long, anthers 0.5 mm long, pale yellow. *Female flowers*: pedicels up to 6 mm long, jointed; sepals 5–9 × 3–4 mm, ± biseriate, triangular-ovate, sericeous-pubescent; disc crenulate; ovary 2 mm long, somewhat 3-lobed, fulvous, hirsute; styles 3 mm long, spreading or recurved, abaxially pubescent, yellow. *Fruit* a capsule, 6–7 × 10–13 mm, 3-lobed, hirsute, green, with velvety golden hairs when young. *Seeds* 5 × 4 mm, subglobose, smooth, brown-marble. *Flowering time*: September–October. Plate 2372.

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PLATE 2373 *Adenia repanda*

Adenia repanda Passifloraceae

Southern Africa

Adenia repanda *(Burch.) Engl.* in Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 14: 375 (1891). *Paschanthus repandus* Burch. in Travels to the Interior of South Africa 1: 543 (1822). *Modecca paschanthus* Harv. in Harvey & Sonder, Flora Capensis 2: 500 (1862) nom. illegit. *Jäggia repanda* Schinz in Verhandlungen des Botanischen Vereins der Provinz Brandenburg und die angrenzenden Lander 30: 254 (1888). *Paschanthus jäggii* Schinz in Mémoires de l'Herbier Boissier 20: 23 (1900). *Modecca repanda* (Burch.) Druce in Report of the Botanical Exchange Club of the British Isles 5 (1916): 636 (1917).

During a botanical expedition to southern Angola arranged by Brian Huntley, a species of *Adenia* Forssk. growing in dry savanna grassland was collected on 21 January 2010 from the top of Iona Peak on the southern border of Angola (Van Jaarsveld 2010a) (Figure 1). The plants were clearly geophytic (Figure 2) and kept short by fires during the dry winter season. The *Adenia* plants grew scattered throughout the grassland at about 1 800 m elevation, all more or less the same size, with subterranean tubers. The collected plant was grown on at Kirstenbosch National Botanical Garden's succulent collection. It started flowering in summer (Figure 3) and was subsequently illustrated by Marieta Visagie. At first it was thought to represent a species new to science, but upon further investigation and the collection of additional material from two sites in the Kaokoveld in Namibia just southwest from Iona, its flowers and leaves soon revealed its true identity. It represented the variable and widespread *A. repanda* (Burch.) Engl.

Some species, as in the case of our plant, are exceptionally adaptable and are able to adjust their life form according to their habitat. The two sites where the plants occur in Namibia are quite similar to the site at Iona, just north of the Kunene River. The first Namibian site where our species was collected was at Ozorotuuo (on the Otjihipa Mountain) on 28 April 2013 during an expedition to Marienfluss (Figure 4); the second Namibian site was on the adjacent southwestern slopes of Ozorotuuo Mountain peak on 19 May 2018 (Figure 5). On both expeditions the first author (EJvJ) was accompanied by Wessel Swanepoel from Windhoek. This variability and plasticity of *Adenia repanda* was documented by Venter (2018) in the journal *Aloe* where two distinctive narrow-leafed forms of *A. repanda* were depicted: one illustration by Joseph Pohl in Engler (1910) and another by De Wilde (1971) from his revision of the genus *Adenia*.

Adenia is mainly confined to the paleotropics. The centres of diversity are in central Africa, Madagascar and Southeast Asia (De Wilde 1971; Venter 1993). It belongs to the Passifloraceae, a pantropical family with nearly a thousand species arranged in 28 genera and, after molecular investigations, placed within three subfamilies: Malesherbioideae, Passifloroideae and Turneroideae (Tokuoka 2012). The family is best known for its edible member,

PLATE 2373.—1, plant in flower, × 1; 2, longitudinal section of female flower, × 3.5; 3, female flower, × 4; 4, gland, × 2. Voucher specimen: *Van Jaarsveld 22658* in Compton Herbarium, Cape Town. Artist: Marieta Visagie.

FIGURE 1.—Typical habitat of *Adenia repanda* at Iona Peak, southwestern Angola. Photograph: E.J. van Jaarsveld.

FIGURE 2.—*Adenia repanda* collected from Iona Peak, southwestern Angola. Photograph: E.J. van Jaarsveld.

the granadilla or passion fruit (*Passiflora edulis* Sims, subfamily Passifloroideae). *Adenia*, with about 93 species, also belongs to subfamily Passifloroideae (Christenhusz et al. 2017). Ten *Adenia* species occur naturally in Namibia and South Africa (Van Jaarsveld 1987; Smith et al. 1997). Liebenberg (1939) revised the South African species of the genus, and the last monograph of *Adenia* was by De Wilde in 1971, who also wrote up the genus for the *Flora of southern Africa* (1976) and *Adenia* species with succulent features for the *Illustrated Handbook of Succulent Plants* (Eggli 2002).

Adenia repanda belongs to the monotypic section *Paschanthus* (Burch.) Harms (1893), characterised by their subterranean tubers, axillary inflorescences and glands at the base of the leaves. Other tuberous species from the subregion, from the northern and eastern parts of South Africa and

Eswatini, belong to section *Blepharanthes* (J.E.Smith) Miquel; these include *A. digitata* (Harv.) Engl., *A. hastata* (Harv.) Schinz and *A. wilmsii* Harms. The growth forms of the remainder of the South African species are diverse, from lianas such as *A. gummifera* (Harv.) Harms, a rampant-growing, green-stemmed climbing succulent in forests, to thickset shrubs from the dry savanna. Most of the South African species have some tendency to climb. *Adenia fruticosa* Burtt Davy, *A. glauca* Schinz and *A. spinosa* Burtt Davy have large aboveground caudices and occur in dry bushveld in Mpumalanga and Limpopo provinces of South Africa. *Adenia pechuelii* (Engl.) Harms, endemic to the northern Namib Desert, has a large caudex that can grow up to a metre in diameter with many short erect spinescent branches. These caudiciform species, which are popular among succulent plant collectors, are grown for their ornamental value and often have mottled green stems.

FIGURE 3.—*Adenia repanda*, collected at Iona Peak, grown at Kirstenbosch National Botanical Garden. Note the globose shape of the tuber of which the surface is grey with a distinct reticulate-foveate pattern. Photograph: E.J. van Jaarsveld.

Adenia fruits vary in size and colour. They are almost always globose, granadilla-like, with a bright red to yellow pericarp. All parts of *A. digitata* are highly toxic. The fruits of *A. hastata* are apparently edible (Watt & Breyer-Brandwijk 1962). However, all fruits of *Adenia* although colourful, should be avoided and never tasted. According to Watt & Breyer-Brandwijk (1962) *A. repanda* is readily grazed by livestock.

Adenia repanda occurs widespread from its southernmost distribution in the lower Orange River Valley (Northern Cape Province) eastwards to North West and Limpopo provinces of South Africa, and further north into Botswana, Zimbabwe, northern Namibia and southern Angola (Figure 6). It grows at elevations of 500–1 900 m and occurs as far southwest in South Africa as the Pellaberg in Bushmanland. Its habitat is diverse, however, the species is always associated with well-drained sites. The localities in Bushmanland is situated in desert with rainfall measuring 75 mm per annum, on the margin of the winter rainfall zone. *Adenia repanda* is not a soil specialist and grows in a variety of soil types derived from quartzitic sandstone, granite and calcrete. Its active growth is during summer and almost always associated with dry arid savanna and in the west, desert (Mucina & Rutherford 2006). It usually grows as a climber to about 2 m high in shrubs or small trees. Since *A. repanda* occurs widespread and is not threatened, it is listed as Least Concern (LC) in the *Red List of South African Plants* (Raimondo et al. 2009).

FIGURE 4.—*Adenia repanda* in habitat east of the Marienfluss. Photograph: E.J. van Jaarsveld.

FIGURE 5.—*Adenia repanda* growing on the south-western slopes of the Ozorotuuo Mountain. Photograph: E.J. van Jaarsveld.

On a granite hill (Figure 7), just east of Moçâmedes in southwestern Angola, plants were observed growing with various species of *Commiphora* (*C. virgata* Engl., *C. angustifoliolata* Mendes, *C. glaucescens* Engl., *C. steynii* Swanepoel), *Sterculia africana* (Lour.) Fiori, *Euphorbia matabelensis* Pax and *Vachellia reficiens* (Wawra) Kyal. & Boatwr. Succulents growing here include *Tavaresia angolensis* Welw., *Aloe hereroensis* Engl., *Cyphostemma uter* (Exell & Mendonça) Desc., *Euphorbia subsalsa* Hiern, *E. eduardoi* L.C.Leach, *Portulacaria carrissoana* (Exell & Mendonça) Bruyns & Klak, *Cissus cactiformis* Gilg, *Sesamothamnus benguellensis* Welw. and stunted individuals of *Adansonia digitata* L. (Van Jaarsveld 2010a). At Iona Peak (Figure 1) plants were observed amongst grass in savanna and associated with *Senegalia montis-usti* (Merxm. & A.Schreib.) Kyal. & Boatwr.,

Peltophorum africanum Sond., *Turnera oculata* Story var. *paucipilosa* Oberm., *Dalbergia nitidula* Welw. ex Baker, *Commiphora africana* (A.Rich.) Engl. and *Sclerocarya birrea* (A.Rich.) Hochst. Associated succulents include *Cyphostemma currorii* (Hook.f.) Desc., *Kalanchoe lanceolata* (Forssk.) Pers. and *Portulacaria carrissoana* (Exell & Mendonça) Bruyns & Klak. In a grassy habitat (e.g. habitat as pictured in Figure 8), plants are subject to regular winter fires and grazing, ensuring their geophytic existence. *Adenia repanda* was also observed on 26 March 1985 growing on the lower southeastern slopes of Pellaberg, at Swartmodder, Bushmanland in the lower Orange River Valley. Here plants were observed in desert with species such as *Aloidendron dichotomum* (Masson) Klopper & Gideon F.Sm., *Boscia albitrunca* (Burch.) Gilg & Gilg-Ben., *Bowiea volubilis* Harv. ex Hook.f. subsp. *gariepensis* (van Jaarsv.) Bruyns, *Brunsvigia gariepensis* Snijman, *Commiphora gracilifrondosa* Dinter ex Van der Walt, *Eriospermum ernstii* P.L.Perry, *Euphorbia mauritanica* L., *Ficus cordata* Thunb., *Jatropha orangeana* Dinter ex P.G.Mey., *Kleinia cephalophora* Compton, *Larryleachia perlata* (Dinter) Plowes, *Pappea capensis* Eckl. & Zeyh., *Cynanchum pearsonianum* Liede & Meve, *Stapelia similis* N.E.Br. and *Tylecodon rubrovenosus* (Dinter) Toelken.

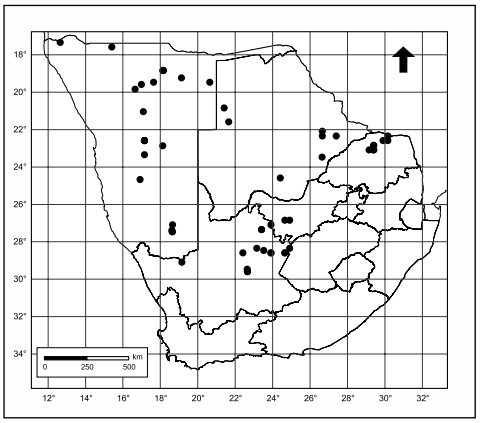

FIGURE 6.—Geographical distribution range of *Adenia repanda* in southern Africa.

Climbers with tuberous roots usually reflect a seasonally dry climate and some woody component in their habitat. Moisture is stored in their tubers to allow plants to go into dormancy for long periods of time, especially in semi-desert conditions with unpredictable and generally low rainfall with periods of drought. During favourable growing conditions, their fast-growing, climbing stems (with tendrils) allow the plants to take advantage of the support of the woody component (trees or shrubs) in its habitat as demonstrated by *Adenia repanda* (Figure 7). The plant thus takes advantage of its host's woodiness to attain its required height and maximise the position of its leaves for photosynthesis, its flowers to possible pollinators and its red fruits for dispersal. Plants growing among grass and subject to regular fires will take on a geophytic lifestyle, the regular pruning by fires causing plants to have shorter annual stems, leaves and flowers. Livestock and game will also keep the arboreal stems trimmed, thus enhancing its geophytic lifestyle. The glaucous leathery leaves (of both growth forms) is a result of a powdery bloom that help plants to reflect sunlight to cool them down. The waxy layer on the leaves also helps to reduce transpiration and subsequent moisture loss. The infolded (canaliculate) margins further reduce transpiration and surface exposure to the sun. Although the stems and leaves are reported to be heavily grazed by livestock (Watt & Breyer-Brandwijk 1962) it is not known whether their tubers, like some other species such as *A. digitata*, are very poisonous. The latter has cyanogenic compounds, a chemical defence strategy that discourages herbivory, especially during the dry season when there is a scarcity of food and water. *Adenia repanda* has another amazing ability to protect its aboveground parts. The nectar produced by the extrafloral nectaries

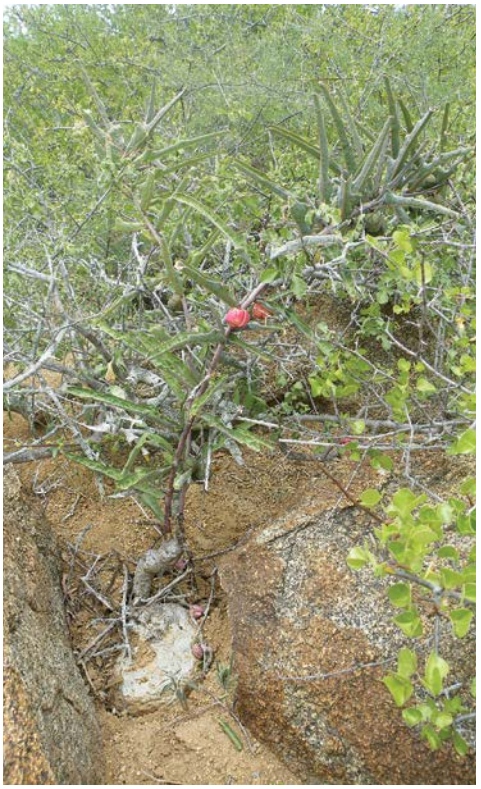

FIGURE 7.—*Adenia repanda* growing among granite rocks, east of Moçâmedes, southwestern Angola. Note the climbing stems making use of the woody component in its immediate habitat for support, and its conspicuous red fruit. Photograph: E.J. van Jaarsveld.

at the base of the leaves provide food for ants, which is mutually beneficial to both organisms, as the ants, in turn, rid the plants of parasites (Benson et al. 1976; Hearn 2006). This feature has been documented in most other *Adenia* species as well. The tubular flowers suggest an insect pollinator, whereas its conspicuous, reddish, three-carpeled fruit with loculicidal dehiscence that expose the seed would attract some animal agent for dispersal (Figure 7). The flattish seeds germinate during the rainy season under favourable conditions.

William Burchell (1781–1863), well-known British traveller and natural history explorer, collected plants of *Adenia repanda* in Griqualand West of the Northern Cape on 16 February 1812 in the Asbestos Mountains near Griekwastad, where he also discovered the first species of *Lithops*. He described his plant under the name *Paschanthus repandus* Burch. in the first volume of his *Travels to the Interior of South Africa* (1822) (Gunn & Codd 1981). The synonymy above reflects its taxonomic history and initial classification chaos within the group. However, stability was brought by Adolf Engler who grouped together all the relevant species under *Adenia* (1891).

The genus name *Adenia* commemorates the city Aden in Yemen in the Arabian Peninsula (Clarke & Charters 2016). The specific epithet, *repanda*, refers to its leaves of which the margin is unevenly or slightly wavy (Daydon Jackson 1917; Usher 1966).

The genus *Adenia* is also popular among collectors of succulents. They are ideal for bushveld or savanna gardens and grown for their ornamental, succulent, mottled green stems (Van Jaarsveld 2010b). Although easily grown, they rapidly rot with too much water (especially during winter, its resting season) or in soil that does not drain well. *Adenia repanda* is also grown with its tuber raised above the soil for effect. In regions outside of its natural habitat, it is best to grow it as a container plant in a glasshouse under controlled conditions. Plants should be kept completely dry during winter.

Description.—Climber (with tendrils) in savanna, growing up to 2 m high, or often remains a geophyte (tendrils absent) in grassland with frequent fires, always with subterranean tuberous root; evergreen under favourable conditions, becoming deciduous during

periods of drought. *Tuber* initially globose, becoming turnip-shaped or elongated, often becoming distorted by its rocky habitat, up to 500 mm in diameter in old specimens; surface grey with a reticulate-foveate pattern. *Branches* terete, green, mottled; up to 10 mm in diameter at base with tendrils up to 50 mm long. *Leaves* ascending spreading, leathery; lamina often canaliculate or infolded, glaucous, linear to obovate 20–150 × 2–20 mm, penniveined (4–10 pairs), veins often purplish, epidermis with a wax layer; base acute to somewhat subcordate; apex obtuse to retuse; margin entire; petiole to 10 mm long, repand, purplish; glands at base of leaf, one at each side of main vein, 1.0–1.5 mm in diameter. *Inflorescence* axillary cymes, sessile to shortly pedunculate, sometimes with short tendril, clustered, 1–5-flowered, polygamous or dioecious. *Male flowers* tuberous infundibuliform, 15–20 × 2–5 mm, greenish cream purplish-mottled; hypanthium 9–14 mm long, tubiform, calyx lobes 5.4–7.5 mm long, oblong-lanceolate obtuse; petals lanceolate, subacute 5–8 × 1.5–2.0 mm, 1–3 nerved, the margin entire or dentate-fimbriate towards apex; filaments 3.5–6.0 mm long, free, inserted about 5 mm above base of hypanthium; anthers 4–6 mm long, obtuse. *Female flowers* tubular campanulate, 8–14 × 3–4 mm; pedicel 1–2 mm long; ovary ellipsoid 2.5–4.0 mm long; style partially connate, 3-armed; stigma subglobose, papillate, 1.0–1.5 mm long. *Fruit* subglobose, 15–30 mm in diameter, pericarp coriaceous, bright red. *Seed* flattened, 2–12 mm long, suborbicular or broadly ovate. *Flowering time*: October to February (in the southern hemisphere). Plate 2373.

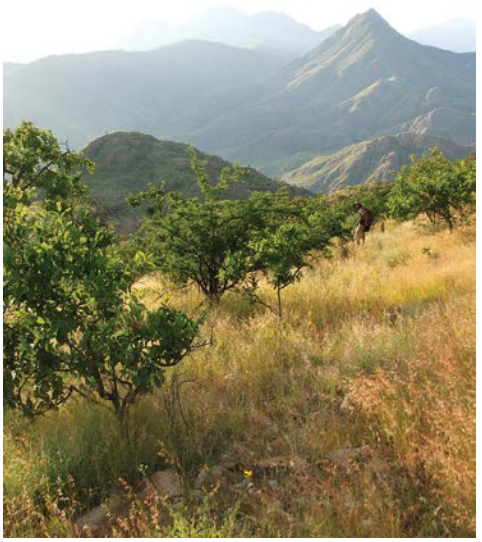

FIGURE 8.—*Adenia repanda* habitat south of Ozorotuuo, Otjihipa Mountain, after the rainy season with plenty of grass, looking towards the north with the distinctive Ozorotuuo crested peak in the background where the plant also occurs. Photograph: E.J. van Jaarsveld.

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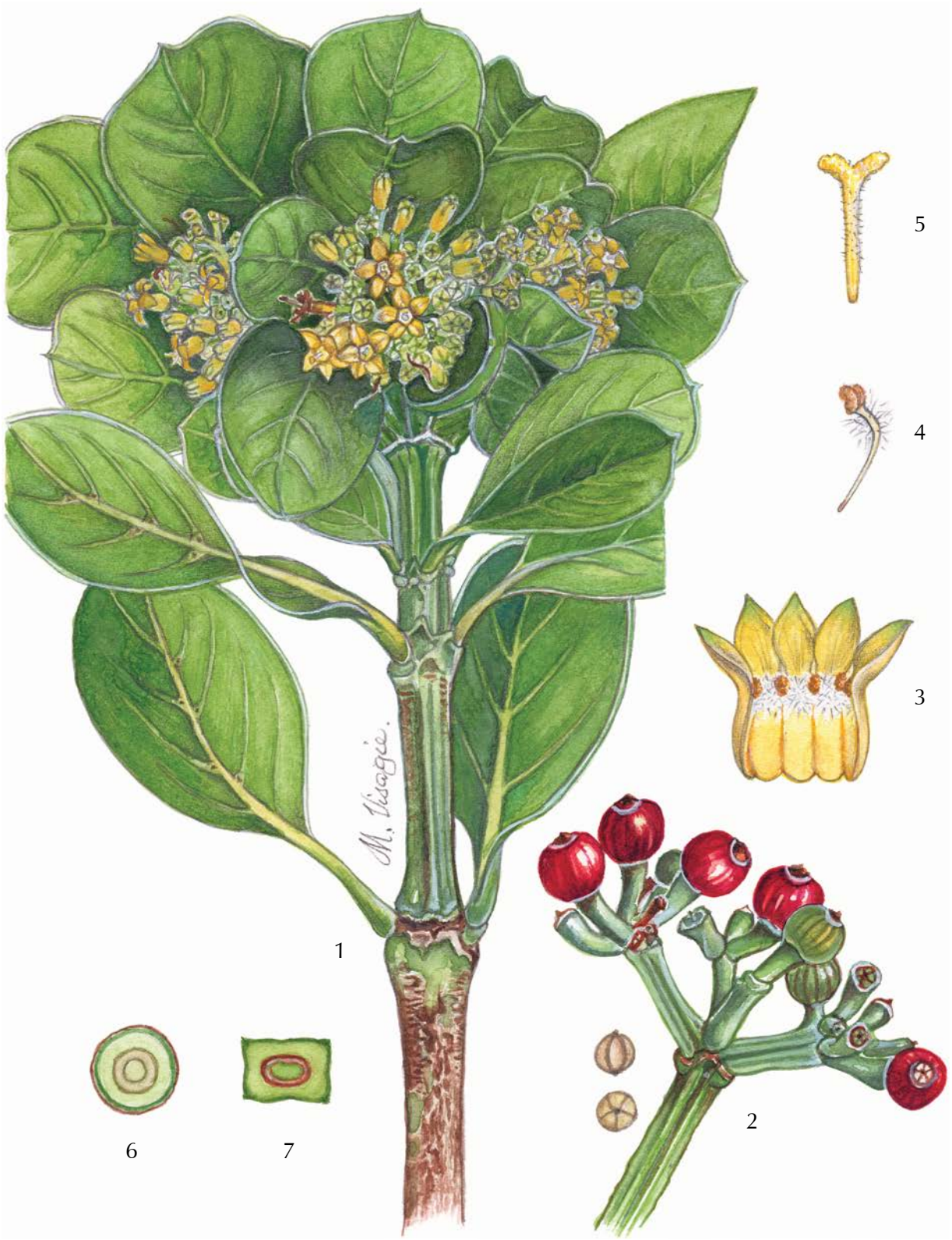

PLATE 2374 *Psychotria suber*

Psychotria suber Rubiaceae

Southern Africa

Psychotria suber *Van Jaarsv. & S.Venter* sp. nov. is distinguished from *P. capensis* (Eckl.) Vatke by its distinctly corky, thick and fissured bark (versus thin and smooth); thickly coriaceous leaves (versus coriaceous) with domatia always present (versus occasional); shortly tomentose pedicel (versus glabrous), angular peduncle (versus terete), larger flowers (10–12 mm in diameter versus 4–5 mm in diameter), villous filaments (versus glabrous) and much longer style (8–10 mm long versus 2–3 mm long).

TYPE.—SOUTH AFRICA, Mpumalanga: Komatipoort, Three Sisters, on the upper southern slope of the highest peak (2531CB), 11 September 2017, *Van Jaarsveld 27428* (PRE, holotype).

Psychotria suber, a new small tree species endemic to the upper granitic mountains east of Mbombela [Nelspruit] in Mpumalanga, South Africa (Figure 1–3) is named. This new species was formerly confused with *P. capensis*, a forest and forest margin species from the eastern parts of South Africa.

Psychotria suber belongs to the Rubiaceae. The Rubiaceae are a large, morphologically diverse family, cosmopolitan in distribution and includes 13 620 species, ranging from small herbs, epiphytes and shrubs to large trees (Christenhusz et al. 2017). Most trees and shrubs in South Africa and Namibia belong to the Rubiaceae family (Van Wyk & Van Wyk 2013). Members of the Rubiaceae are at once recognised by their opposite leaves with stipules between the petioles (interpetiolar) and actinomorphic regular flowers. Various species are of economic, medicinal and horticultural importance. Some well-known products derived from Rubiaceae members include coffee from *Coffea arabica*; Indian tonic (cinchona) and quinine (the antimalarial alkaloid) from the bark of various *Cinchona* species; and a red dye from *Rubia tinctorum*. The family name was derived from *Rubia*, or *ruber* which is Latin for 'red' (Clarke & Charters 2016).

The genus *Psychotria* was established by Linnaeus in his *Species Plantarum* in 1753. It is a large genus, consisting of about 1 858 species, of which most are confined to the tropics. The genus' centre of diversity is clearly in South America (Christenhusz et al. 2017). The generic name *Psychotria* is derived from *psyche*, meaning 'life', which is in reference to the healing properties of some species (Clarke & Charters 2016). The hallucinogenic drug ayahuasca is used in South America and derived from *Psychotria viridis* and one or two other main ingredients. Ipekakuana, a powerful emetic, is a product from *Psychotria* species. About 200 species of *Psychotria* have been recorded for Africa south of the Sahara (Klopper et al. 2006), of which only five taxa are from southern Africa (Coates Palgrave 2005).

Psychotria suber is known from the southern mountains of the Mpumalanga Drakensberg Escarpment and adjacent territory, more or less from Mbombela (formerly Nelspruit),

PLATE 2374.—1, flowering branch, × 0.25; 2, infructescence, × 1; 3, perianth, × 4; 4, stamen, × 5; 5, stigma, × 3; 6, section through young stem, × 1; 7, section through second year branch, × 2. Voucher specimen: *Van Jaarsveld 27428* in National Herbarium, Pretoria. Artist: Marieta Visagie.

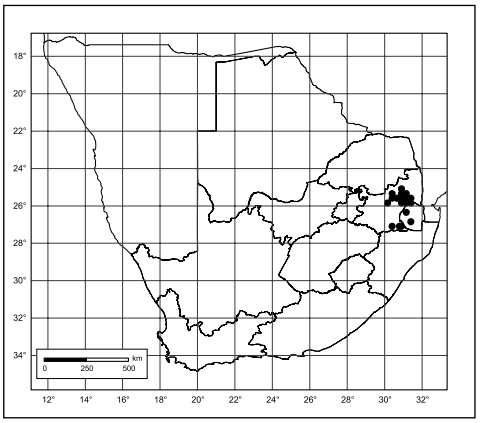

FIGURE 1.—Known geographical distribution of *Psychotria suber.*

Sabie and Kaapmuiden in the north, to the eMkhondo [Piet Retief] district in KwaZulu-Natal as well as Mbabane in Eswatini in the south (Figure 1). Its habitat includes the Mesic Highveld Grassland and Lowveld bioregions. It has been recorded on both igneous and sedimentary formations, from shales, conglomerates, sandstones and siltstones of the Moodies Group of the Barberton Greenstone Belt, to granite. *Psychotria suber* grows in open savanna and grassland on exposed, usually rocky, mountain slopes at altitudes of 800–1 500 m above sea level. It grows mostly in gritty, sandy loam to loamy soils. The vegetation of the region consists of Kaalrug Mountain Bushveld (Lowveld Bioregion), as well as Barberton Montane Grassland and KaNgwane Montane Grassland (Mucina & Rutherford 2006). Although not confined to it, the distribution of *P. suber* falls within the Barberton Centre of Plant Endemism (Van Wyk & Smith 2001). Rainfall for the region is mainly during the austral summer and ranges from 650–1 200 mm per annum. Winters are warm during the day and cold at night with frost rarely encountered. Associated trees and shrubs at the type locality (Three Sisters) include *Aloe arborescens* Mill., *Burchellia bubalina* (L.f.) Sims, *Ekebergia pterophylla* (C.DC.) Hofmeyr, *Pavetta edentula* Sond., *Greyia sutherlandii* Hook. & Harv., *Cephalanthus natalensis* Oliv., *Englerophytum magalismontanum* (Sond.) T.D.Penn. and *Senecio barbertonicus* Klatt. Other smaller, more herbaceous species include *Plectranthus purpuratus* Harv. subsp. *montanus* Van Jaarsv. & T.J.Edwards, *Xerophyta retinervis* Baker, *Merwilla plumbea* (Lindl.) Speta, *Aloe simii* Pole-Evans, *Aloe spicata* L.f., *Aloe rouxii* Van Jaarsv., *Cotyledon egglii* Van Jaarsv. and *Thorncroftia lotterii* T.J.Edwards. The vegetation of the region is subject to regular fires with most species resprouting after fire. The immature green fruits ripen, becoming yellow and finally red, and are dispersed by frugivorous birds.

Psychotria suber is known from a number of populations, some which are located in formally protected areas. e.g., Songimvelo Game Reserve and Mountainlands Nature Reserve, Barberton. Both reserves protect large populations of this species. No formal Red Listing efforts have been made and a suggested preliminary conservation status of Least Concern (LC) is suggested (IUCN 2019).

The specific epithet, *suber*, is from Latin and means 'corky', in reference of the thick and corky bark of the species' stems and branches.

In the past *Psychotria suber* was confused with *P. capensis* subsp. *capensis* var. *capensis*, the latter being a forest and forest margin species from the eastern parts of South Africa. The two species are similar in their yellow flowers and red fruits, but differ significantly in a number of leaf, inflorescence and fruit characters (Table 1). The new species is further distinguished from *P. capensis* subsp. *capensis* var. *capensis* by its distinctly thick, corky fissured bark; larger, obovate leathery leaves; and larger flowers (Table 1; Figure 2 & 3).

Key to the South African species of *Psychotria*:

1a Bark thick and corky, deeply fissured; flowers 10–12 mm in diameter, peduncle branches quadrangular . . . . . *P. suber*

1b Bark thin, smooth to finely fissured; flowers 5 mm in diameter or smaller, peduncle branches terete 2

2a Leaves with 10–16 secondary veins; veins on adaxial lamina surface immersed; inflorescence drooping; flowers pale yellow or white . . . . . *P. zombamontana*

2b Leaves with 4–6 secondary veins; veins on adaxial lamina surface not immersed; inflorescence erect; flowers yellow. 3

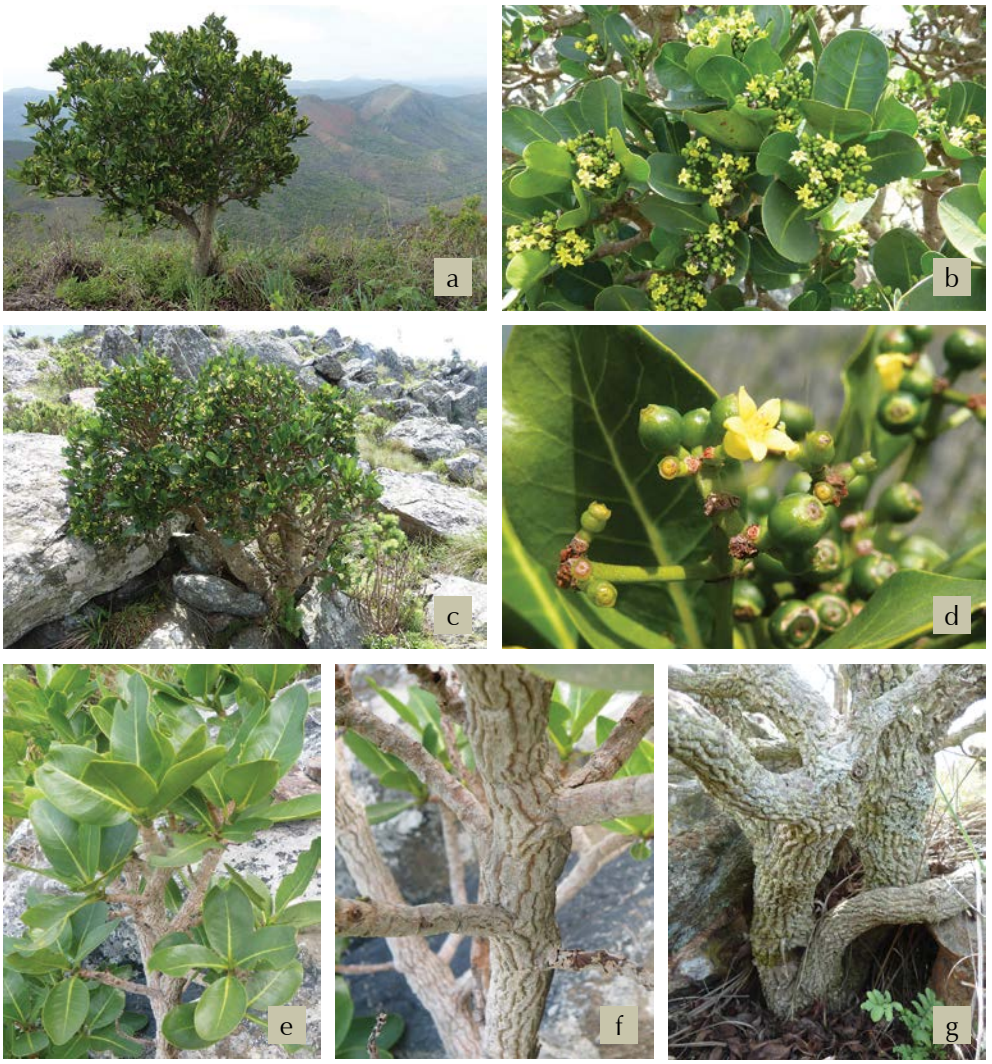

FIGURE 2.—*Psychotria suber*: a, fully-grown tree in natural habitat; b, flowering branches; c, shrub form with more stout stems and branches; d, flowers and young fruit; e, branches showing the thickly leathery leaves; f, thick corky bark; g, stems of the multi-stemmed shrub form showing the corky bark. Photographs: E.J. van Jaarsveld.

3a Inflorescence hairy. . . . . *P. capensis* subsp. *capensis* var. *pubescens*
3b Inflorescence glabrous . . . . . .*P. capensis* subsp. *capensis* var. *capensis*

Additional specimens examined

ESWATINI. **2631** (Mbabane): 3 miles north-east of Mbabane (–AC), *Miller 5/117* (PRE); 2 miles west of Mbabane (–AC), *Hardy 1638* (PRE); Hlatikulu towards Sitobela (–CD), *Ross 1757* (PRE).

SOUTH AFRICA, KwaZulu-Natal: **2730** (Vryheid): Kwa-Madlangampisi, Farm Groothoek (–AB), *Du Toit 41* (PRE); Mooihoek (–BA), *Devenish 1358* (PRE); Bloemendal, 32 km SE of Piet Retief (–BB), *Bremer, Kornhall & Bester* 4303 (PRE). **2830** (Dundee): Kaffir Drift, Utrecht (–CA), *Thode A275* (PRE).

SOUTH AFRICA, Mpumalanga: **2530** (Lydenburg): Schoemanskloof (–AD), *Smuts 333* (PRE); Amajuba Mountain Schagen (–BD), *Liebenberg 3076* (NBG); Sabie towards Rosenhaugh (–BB), *Louw 2755* (NBG); Waterval Onder (–CB), *Jacobsen 4866* (PRE); 18 miles south-east of Sewefontein (–CC), *Codd 8117* (PRE); Berlin, Godwana River Station (–DA), *Hofmeyer 4* (PRE); 14 km from Nelspruit towards Barberton (–DB), *Coetzer 115* (PRE); Stella Mine, Kaapse Hoop (–DB), Nelshoogte (–DD), *Barker 10032* (NBG); Nelshoogte (–DD), *Joubert 13582* (PRE). **2531** (Komatipoort): White River (–AC), Eureka City, Sheba Hills, Barberton (–CA), *Scheepers 4074* (PRE); *Rogers 20442* (PRE); Three Sisters Farm, Louws Creek (–CB), *Jordaan 3725* (PRE); Between Komati River and Barberton (–CC), *De Winter 7993* (PRE); Barberton (–CC), *Smith 7077* (PRE); Barberton (–CC), *Rogers 18235* (PRE); Barberton (–CC), *Pott 5453* (PRE); Drakensberg Escarpment, Barberton (–CC), *Acocks 12754* (PRE); Havelock Mine (–CC), *Miller 3045* (PRE); Kangwane, Songivelo Game Reserve, Schoonoord (–CC), *Dryer 291* (PRE); Kangwane, Songivelo Game Reserve, Schoonoord (–CC), *Germishuizen 5808* (PRE); Nelspruit (–CC), *Britten 4788* (PRE); Near Angle Station, Barberton (–CC), *Moll 6025* (PRE); Twello, Sappi Plantation (–CC), *Bester 1210* (PRE); Songivelo Game Reserve (–CD), *Reid 1878* (PRE); 3 miles west of Piggs peak (–CD), *Codd 7828* (PRE).

TABLE 1.—Differences between *Psychotria suber* and *P. capensis*

Character	***P. suber***	***P. capensis***
Bark	Thick and corky; deeply fissured	Thin; smooth to finely fissured
Lamina texture	Thickly coriaceous	Thinly coriaceous
Peduncle shape in cross section	Quadrangular to subterete	Terete
Flower diameter (mm)	10–12	4–5
Pedicel length (mm)	4–5	0–2
Pedicel indumentum	Shortly tomentose	Glabrous (except in var. *pubescens*)
Calyx external indumentum	Minutely hispid	Glabrous
Calyx lobe length (mm)	1.3–1.5	0.3–0.5
Corolla tube length (mm)	6	1.5–3.0
Filament indumentum	Villous	Glabrous
Fruit diameter (mm)	8–9	5.0–6.5

Description.—Shrub to small tree 2–4 m tall, with a rounded crown. *Branchlets* quadrangular to subterete, green becoming greyish brown, 8–10 × 7–8 mm near apices. *Bark* thick, distinctly corky and longitudinally fissured. *Leaves* clustered towards the tips of the branches, decussate, spreading; stipules triangular, thickly textured, 3–5 mm long and wide, glabrous, apices entire; petiole short, 10–30 × 3–6 mm, glabrous; lamina thickly

FIGURE 3.—*Psychotria suber* in habitat in the Krokodilpoort (formerly known as Moederlief) Nature Reserve: a, plant growing among granite boulders; b, distinctive corky bark; c, plant in fruit. Photographs: K. Balkwill.

coriaceous, obovate to almost sub-orbicular, rarely acuminate, 110–160 × 60–80 mm; base cuneate; margin entire, yellowish; apex obtuse, subacute, subtruncate to emarginate; adaxial surface glabrous, midrib 4–6 mm in diameter, secondary veins raised, 6–8 per side and yellowish; abaxial surface glabrous with raised green veins and domatia in the main vein axils, domatia oval to rounded with tufts of hair. *Inflorescence* terminal, subglobose panicle, 45–100 × 80–90 mm, 40–60-flowered; peduncle 18–45 × 3–5 mm in diameter at base, quadrangular; pedicels 4–5 × 1.8 mm, shortly tomentose. *Calyx* synsepalous, persisting, lobes free in the distal third, minutely hispid, lobes 1.3–1.5 mm long. *Corolla* 5-merous, yellow, 10–12 mm in diameter, tube campanulate, 6 × 4 mm, glabrous outside, inside densely villous in the upper half, lobes ovate, 4.5–5.0 × 3.5 mm, glabrous, apices acute. *Androecium* of five stamens inserted just below the sinuses, anthers smooth, 1.5 × 0.8 mm, semi-exserted in shortly styled flowers, filaments villous. *Gynoecium* glabrous, heterostyled: style 8–10 mm long (long-styled flowers), and 5 mm long (short-styled flowers), thickened towards the stigma, yellowish green, densely puberulous; stigma bilobed, densely papillate, each lobe 1 mm long, yellow; ovary 2-locular, 2 × 2 mm. *Fruit* globose, 8–9 mm in diameter, red, fleshy, glabrous, pedicels 4–5 mm long, shortly tomentose. *Pyrenes* 2 per fruit, flattened, semi-lunar, dorsally costate 5 × 3 mm. *Flowering time*: November to December in the wild, fruits appearing during late autumn and winter. Plate 2374.

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Carissa sebrabergensis Apocynaceae

Namibia

Carissa sebrabergensis *Van Jaarsv. & Swanepoel* sp. nov., differs from *C. bispinosa* by its much smaller size; its ascending, zig-zagging, layered stem ramifications; consistently much smaller leaves of 10–17 × 6–7 mm; smaller, round berries of 10 mm in diameter; and unique habitat among anorthosite boulders in semi-arid savanna.

TYPE.—Namibia (1713): Sebraberg, Kloofsonderend, south-facing slopes (–BC), 1 400 m, 29 May 2012; *Van Jaarsveld*, *Swanepoel*, *Nanyeni* & *Nicolson 24476*, (WIND, holo.!).

Carissa sebrabergensis (Figures 1–4) is named as new from the Sebraberg (Zebra Mountains) in northern Namibia. Features which distinguish it from *C. bispinosa* include its generally smaller size; ascending, zig-zagging, layered stem ramifications; small, leathery leaves; and rounded berries. These features are retained in cultivation.

Carissa belongs to the family Apocynaceae, a large cosmopolitan family with about 322 genera and 4 300 species (Christenhusz et al. 2017). This morphologically diverse family was divided into five subfamilies: Rauvolfioideae, Apocynoideae, Periplocoideae, Secamonoideae and Asclepiadoideae. *Carissa* belongs to subfamily Rauvolfioideae and was established by Linnaeus in 1767. The genus consists of about 35 shrubby species and the type, *C. carandas* L., is from India. The generic name, *Carissa*, is the Sanskrit name for a species in India (Clarke & Charters 2016).

Six species of *Carissa* are recorded for South Africa and Namibia (Coates Palgrave 2002; Van Wyk & Van Wyk 2013). The South African and Namibian species include *C. bispinosa* (L.) Desf. ex Brenan, *C. haematocarpa* (Eckl.) A.DC., *C. macrocarpa* (Eckl.) A.DC., *C. spinarum* L., *C. tetramera* (Sacleux) Stapf and *C. wyliei* N.E.Br. In the revision of *Carissa* by Leeuwenberg & Van Dilst (2001), *C. haematocarpa* and *C. wyliei* was synonymised under *C. bispinosa*. This arrangement, however, was not followed by Coates Palgrave (2002), nor by Van Wyk & Van Wyk (2013) and the authors of this text, similarly, retain the two species. These species grow in a variety of habitats, from the semi-desert Karoo, through the Highveld inland region, to the subtropical coast, with one species confined to lowland forest. All *Carissa* species produce edible fruit. The largest and most popular species, *C. macrocarpa*, is known in South Africa as num-num or *noem-noem* (Afrikaans), which, according to Smith (1966) was recorded by the early explorers Thunberg and Burchell (Burchell 1822–1824) and is derived from the plant's Koi name (Smith 1966). *Carissa macrocarpa*, originally indigenous to the Eastern Cape and coastal KwaZulu-Natal, has become a favourite plant in ornamental horticulture and is grown worldwide. Only *C. bispinosa*, *C. haematocarpa* and *C. spinarum* have been recorded for Namibia (Mannheimer & Curtis 2009; Bruyns 2014).

PLATE 2375.—1, flowering and fruiting branch, × 1; 2, forked and simple spine, × 2; 3, gynoecium, × 12; 4, longitudinal slit through corolla, × 4.5; 5, corolla with calyx removed, × 4; 6, fruit, × 1; 7, dried fruit, × 5.5; 8, mature fruit, × 4. Voucher specimen: *Van Jaarsveld 28242* in Compton Herbarium, Cape Town. Artist: Marieta Visagie.

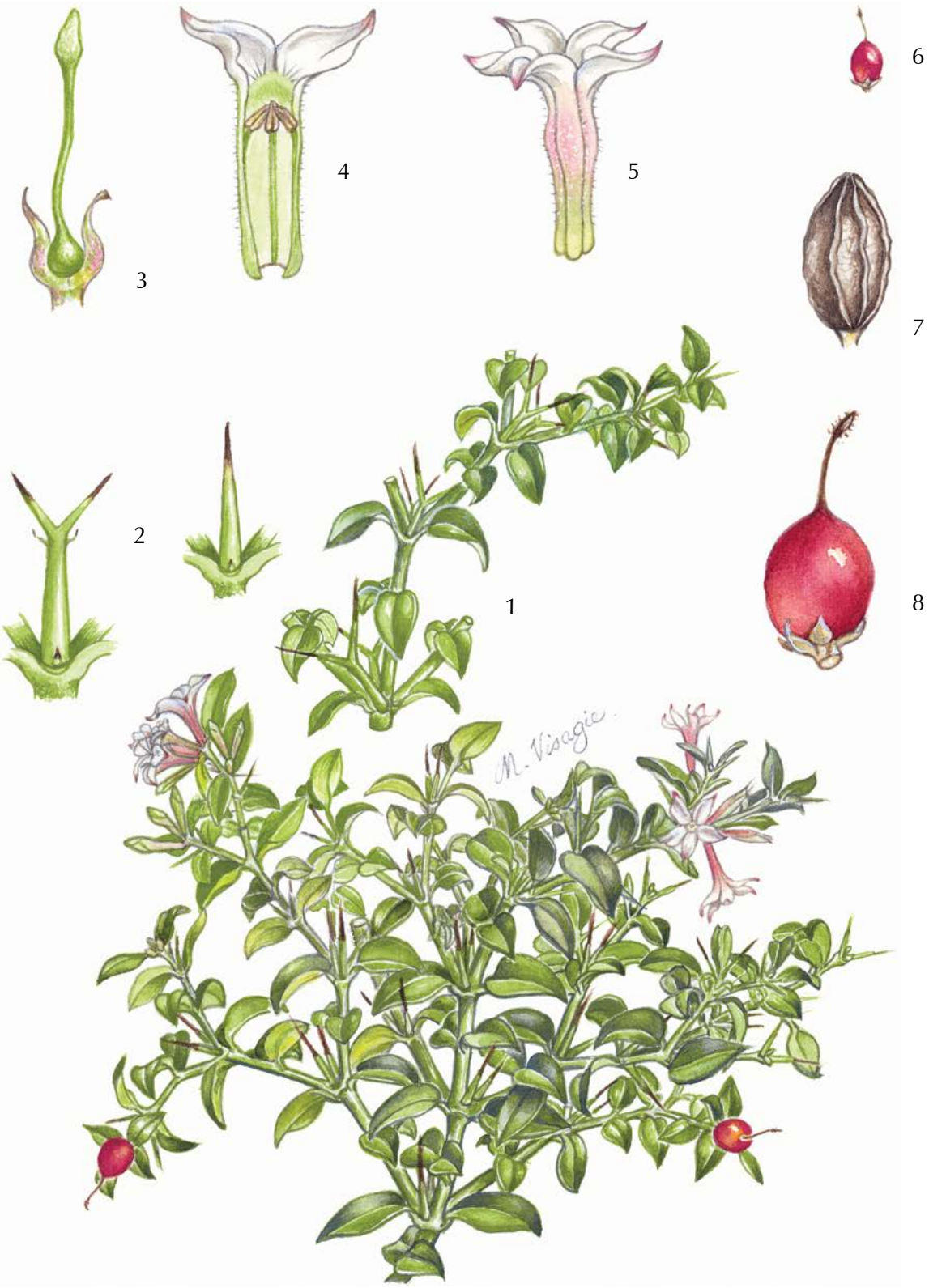

PLATE 2375 *Carissa sebrabergensis*

FIGURE 1.—*Carissa sebrabergensis* fruit: a, fruiting branches; b, close-up of globose, glossy berry. Photographs: E.J. van Jaarsveld.

On an expedition to Namibia in May 2012, two of us (Swanepoel & Van Jaarsveld) jointly decided to investigate the, hitherto unknown, Sebraberg, a geologically unique formation consisting of igneous anorthosite of the Kunene Complex (Miller & Schalk 1980, Mendelsohn et al. 2002) – one of the largest anorthosite massifs on Earth (up to 18 000 km^2). Liudmila Ozepowa from the Moscow Botanical Garden, Leevi Nanyeni from the Namibia Botanical Research Institute and Gregory Nicolson, freelance ecologist from the Western Cape, South Africa, also joined us. The igneous rock weathers into rounded boulders with vertical streaks of scree slopes, not unlike dolerite, and that led to the name Sebraberg. We investigated both the southern and northern portions of this mountain complex and were surprised to find interesting new taxa (e.g. *Maerua sebrabergensis* Swanepoel; others still in preparation) and new distribution records.

As we ascended Kloofsonderend, a boulder-strewn kloof on the southern slope, a species of *Carissa* was found growing with *Euclea divinorum* Hiern and *Croton gratissimus* Burch. Its leaves were markedly smaller than those of the widespread *Carissa bispinosa* and its zig-zagging, layered, ascending, spreading branches were distinct; it also had rounded fruits, 10 mm in diameter (Figure 1). Specimens were prepared, and seed and cuttings gathered of which both were later grown and rooted at Kirstenbosch National Botanical Garden. Here the plants retained their small leaves and other diagnostic vegetative and floral features. When the plants came into flower in 2017, a voucher was given to Marieta Visagie to illustrate. Meanwhile a description was prepared and the new species named for its Sebraberg habitat in the northern Kaokoveld, Namibia (Figure 2).

We climbed to the highest peak in the southwest where we encountered *Celtis africana* Burm.f. and *Chaetachme aristata* Planch. belonging to the Cannabaceae (formerly sorted

under the Ulmaceae), both first records for Namibia. Here we also encountered *Brachylaena huillensis* O.Hoffm., *Nuxia congesta* R.Br. ex Fresen. and *Ricinus communis* L. As we ascended the peak, Wessel Swanepoel heard and spotted the Angola Cave Chat, *Xenocopsychus ansorgei* (Hartert, 1907), the first record of this bird for Namibia. Along a stream bank on the northern portion of the Sebraberg we also encountered a potentially new species of *Ocimum* and in one of the intermontane plains, potentially new species of *Premna* and *Distephanus* were discovered. The vegetation of the Sebraberg, in general, compared to the surrounding mopane savanna is extremely spiny and the best way to access certain areas is to remain in the boulder fields. This spinescent vegetation is an example of mechanical defence in reaction to herbivory, as the fertile soil (known as sweet veld) support various palatable grass, shrub and tree species. The tree and shrub vegetation of the Sebraberg consists of *Combretum apiculatum* Sond., *Spirostachys africana* Sond., *Kirkia acuminata* Oliv. and various *Commiphora*, *Senegalia* and *Vachellia* species; the vegetation of the intermontane plains consists mainly of mopane savanna with *Colophospermum mopane* (J.Kirk ex Benth.) J.Kirk ex J.Leonard the dominant tree. The boulder fields consists of thickets with, among other plants, *Aloe littoralis* Baker, *Adenium boehmianum* Schinz, *Croton gratissimus*, *Cyphostemma currorii* (Hook.f.) Desc., *Entandrophragma spicatum* (C.DC.) Sprague, *Euphorbia eduardoi* L.C.Leach, *Ficus bubu* Warb., *F. glumosa* Delile, *Pappea capensis* Eckl. & Zeyh., *Steganotaenia araliacea* Hochst., *Moringa ovalifolia* Dinter & A.Berger, *Sterculia africana* (Lour.) Fiori, *S. quinqueloba* (Garcke) K.Schum., *Adansonia digitata* L. and

FIGURE 2.—*Carissa sebrabergensis* in habitat on the Sebraberg, Kaokoveld, northwestern Namibia. Photograph: E.J. van Jaarsveld.

a potentially new species of *Sesamothamnus*. Spiny elements of Sebraberg vegetation encountered include *Senegalia mellifera* (Vahl.) Seigler & Ebinger subsp. *detinens* (Burch.) Kyal. & Boatwr., *S. ataxacantha* (DC.) Kyal. & Boatwr., *Chaetacme aristata* Planch., *Obetia carruthersiana* (Hiern) Rendle, *Sansevieria pearsonii* N.E.Br., *Vachellia kirkii* (Oliv.) Kyal. & Boatwr. and species of *Solanum*, *Barleria* and *Hibiscus*.

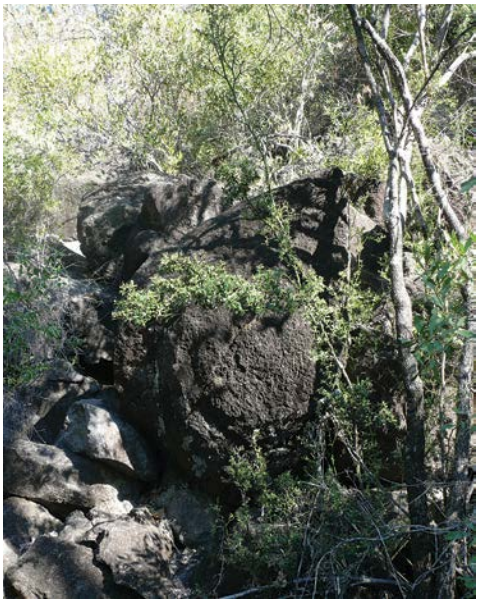

FIGURE 3.—*Carissa sebrabergensis* in typical habitat, among anorthosite boulders in a kloof. Photograph: E.J. van Jaarsveld.

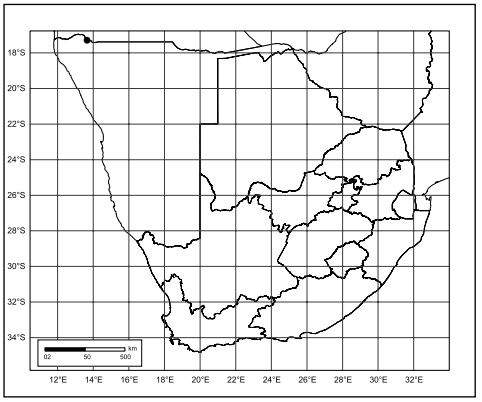

FIGURE 4.—Distribution of *Carissa sebrabergensis*, only known from anorthosite boulder kloofs and fields of the Sebraberg, northwestern Namibia. Since the anorthosite continues on the northern side of the Kunene River, the species may eventually prove to occur in Angola as well.

Carissa bispinosa is the most widespread and common *Carissa* in southern Africa and immediately identified by its spines that are forked once, white flowers of which the tube is 6–9 mm long and the lobes up to 5 mm long, and ovate red fruit that are 10–16 mm long. The species also grows in the southeastern and eastern parts of the subcontinent with a few records from northern Namibia, in subtropical thicket and savanna. Furthermore, *C. bispinosa* is a very variable taxon and represent the closest match for our new species. So, when is a new taxon justified? A name provides a 'handle' to identify a plant, so that anyone else can clearly recognise it as a unique entity. In the horticultural trade such a distinguishing characteristic can be the slightest variation in colour or shape of plant organs, fruit taste, or other features. A cultivar name, in inverted commas after the binomial name, designates such a cultivated status. Such a cultivar can be the result of a hybrid, mutation (such as variegation), or simply genetic variability within the cultivated plant. In the field, however, different criteria are in place. No efficient species definition is known and in many cases species are very difficult to determine with certainty. Thus the barriers of species definition is not always clear cut and depend on a number of variables specific to the taxon under investigation. For a species new to science, criteria should be easily recognisable, based on unique morphological characteristics and not simply a continuation of variation, which is usually used in describing a new subspecific entity. In naming a new subspecies, geographic separation from its closest

relative is usually a reliable and good character. Our new species is clear cut, remains genetically distinct in cultivation and can be recognised as different from *C. bispinosa* at once: it has a dwarf stature (usually under a metre in height); its branches are uniquely layered, often zig-zagging; its fruits are rounded to rounded-oval, up to only 10 mm in diameter; and its distribution is confined to a unique geological formation, as it is only known from the Sebraberg, growing among anorthosite boulders (Figure 3) in semi-arid savanna. Since the anorthosite continues on the northern side of the Kunene River, the species may eventually prove to occur in Angola as well (Figure 4).

The habitat of *Carissa sebrabergensis* lies well within the tropics with the rainfall (through convectional rain) measuring between 100–400 mm per annum, received mainly during the summer and autumn months of the southern hemisphere. Summers are very hot and winters hot, but cool during the evenings without frost (Mendelsohn et al. 2002).

Carissa sebrabergensis grows well in cultivation, both in containers and out of doors. As with other species of *Carissa*, it is easily propagated from stem cuttings or seed. With its layered evergreen growth of small glossy leaves, fragrant white flowers and red berries, it is a decorative little shrub. It makes for a great waterwise garden plant as it can withstand heat and drought. Plants grown in the biomes garden of the Babylonstoren Farm near Paarl (Western Cape Province, South Africa) during the summer drought of 2017–2018 grew well without being watered.

Description.—Evergreen much-branched (dichotomously) leafy spiny shrub, to 1 m tall from a solitary stem. *Young stems* ascending with zig-zagging and layered ramification; surface green, minutely puberulous; older stems becoming grey. *Sap* milky. *Main branch* 25 mm in diameter at base, often with erect side shoots arising from near base; bark grey, wrinkled; spines simple to once forked, 5–7 mm long, persistent. *Leaves* ascending spreading, leathery, linear ovate, 10–17(–18) × (2–)6–7 mm; petiole short, to 1 mm long; lamina sparsely puberulous becoming glabrous with a shiny surface, paler below, margin semi-translucent, minutely ciliolate, main vein semi-translucent; base rounded to obtuse; apex acute with sharp mucro pointing down. *Flowers* in terminal clusters; bracts ovate acuminate, 1.5–2.0 × 0.5 mm; calyx 3 mm long, lobes lanceolate acuminate, 1.5 mm long, sparingly beset with glandular hairs; corolla white, salver-shaped, up to 9 mm in diameter; tube slender 5.3–7.2 × 1.4–1.6 mm, minutely pilose, throat beset with longer white hairs 0.5 mm long; lobes ovate lanceolate, spreading 3–5 × 1.3–1.8 mm. *Stamens* 5, inserted at the top of the tube. *Gynoecium* 4.1 mm long; ovary entire, 2-chambered; style filiform; stigma stipitate. *Fruit* globose, 10 mm in diameter, more or less of the same length, glossy, red, 1–2-seeded. Plate 2375.

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Alectra vogelii Orobanchaceae

Sub-Saharan Africa

Alectra vogelii *Benth.* in A.DC., Prodromus systematis naturalis regni vegetabilis 10: 339 (1846); Hemsley & Skan: 368 (1906); Melchior: 432 (1941); Hepper: 368 (1963); Philcox: 91 (1990); Merxmüller & Roessler: 8 (1967); Fischer: 287 (2006); Morawetz: 183 (2007); Ghazanfar et al.: 114 (2008). *Alectra hirsuta* Klotzsch in Peters: 221 (1862). *Alectra hippocrepandra* (Hiern) Hemsley in Hemsley & Skan: 367 (1906). *Melasma hippocrepandra* Hiern: 768 (1898). *Alectra picta* (Hiern) Hemsley in Hemsley & Skan: 368 (1906). *Melasma pictum* Hiern: 770 (1898). *Alectra lancifolia* Hemsley in Hemsley & Skan: 367 (1906). For additional synonyms see Morawetz (2007).

Molecular studies at the beginning of the 21st century have led to a revised and considerably expanded circumscription of the Orobanchaceae. This family now includes all photosynthetic and non-photosynthetic root-parasitic members of the former Scrophulariaceae and Orobanchaceae, in addition to a non-parasitic genus, *Lindenbergia* (Olmstead et al. 2001; Schneeweiss 2013). Currently two further non-parasitic genera are also classified in Orobanchaceae, namely *Rehmannia* and *Triaenophora*, these representing a second non-parasitic clade which is sister to all other Orobanchaceae (Albach et al. 2009; Xia et al. 2009; Schäferhoff et al. 2010). The Orobanchaceae have a cosmopolitan distribution and is the largest of the about 20 eudicot flowering plant families that contain parasitic plants (Joel et al. 2013). Parasitic plants can be classified into two broad groups, those that are photosynthetic, called hemiparasites; and those that are not, called holoparasites, the latter which are completely dependent on their hosts for carbon (Heide-Jørgensen 2013).

Alectra, a genus of primarily obligate hemiparasitic herbaceous species, was described by Carl Peter Thunberg (1784) based on the South African species *Alectra capensis*. The derivation of the generic name remains the subject of speculation. According to Jackson (1990) and Clarke & Charters (2016) the name is derived from the ancient Greek *alektor/alektryon*, a rooster, because of the flowers' similarity to a cock's comb. However, although the most popular explanation, such a resemblance is not too obvious, unless it is ascribed to the five triangular calyx lobes, but even then some imagination is required. Another (rather fanciful) explanation is that the name is derived from the Greek *alectros* = unwedded; from *a* = without + *lektron* = coach, bed, marriage-bed (Genaust 1996; Quattrocchi 2012).

In the most recent monograph of *Alectra*, 11 species and six varieties were recognised (Morawetz 2007), distributed mainly in sub-Saharan Africa and Madagascar, with two species indigenous to tropical America, and two widespread species extending out of Africa

PLATE 2376.—1–3, flowering shoots (showing variation in same clump of plants) with red pigmentation of green tissues lacking (1), moderately present (2), or abundantly present (3), × 2; 4, flower with bracteoles, in side view (showing bright red streaks), × 2; 5, calyx opened out, × 2; 6, corolla with androecium opened out, × 2; 7, stamens, × 10; 8, gynoecium on pedicel (other floral whorls not shown), with ovary sectioned longitudinally and parallel to septum, × 4; 9, capsule (marcescent corolla removed), with seeds spilling out, × 2; 10, seeds, × 10. Voucher specimen: *Hyde-Johnson 120* in H.G.W.J. Schweickerdt Herbarium, Pretoria. Artist: Jenny Hyde-Johnson.

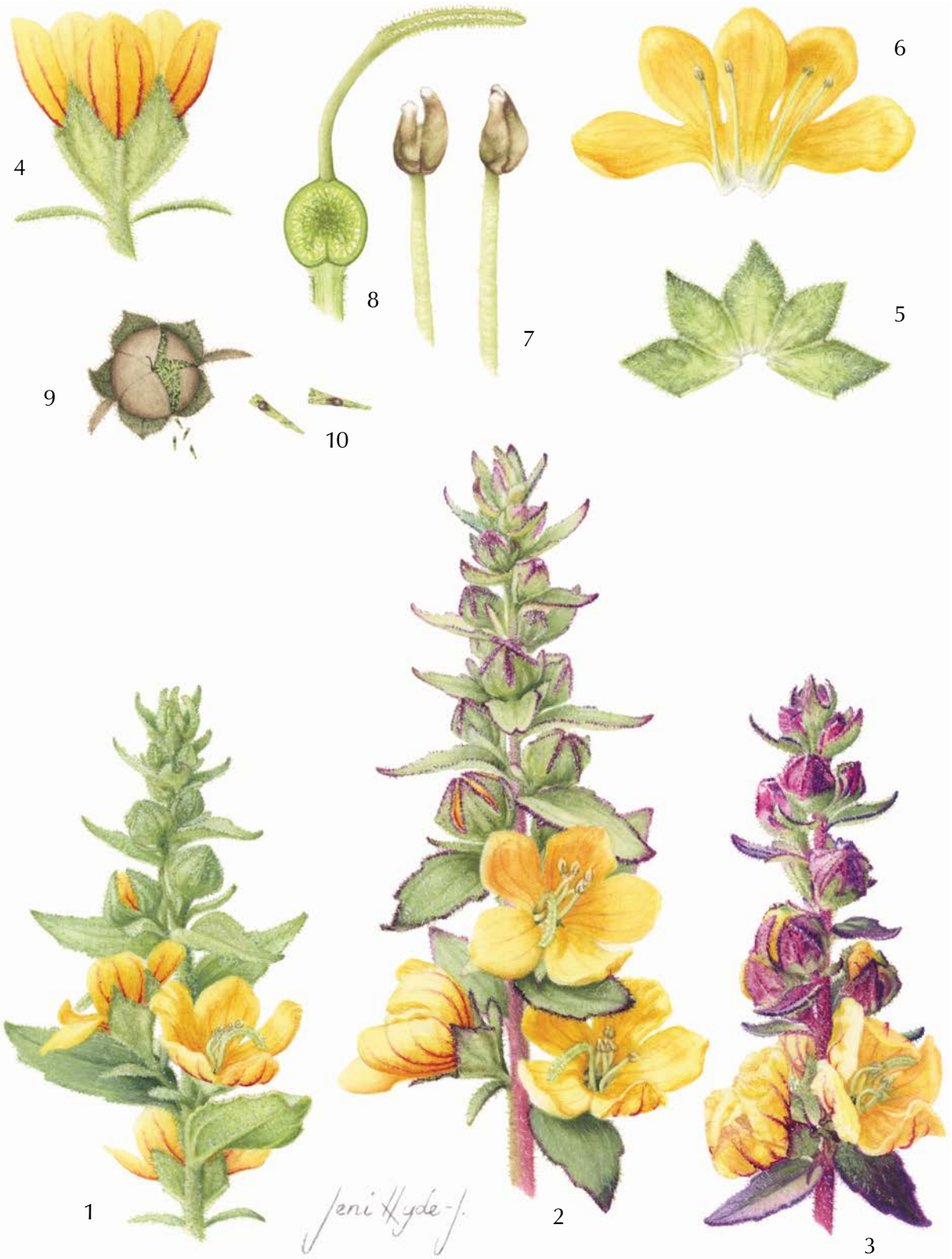

PLATE 2376 *Alectra vogelii*

through the Middle East into India, China and the Philippines. This is a considerable reduction in the number of species compared to the 41 recognised by Melchior (1941) in the first monograph of the genus. Prior to Morawetz's monograph, Melchior's classic treatment has been widely followed and a number of additional new species and infraspecific taxa were subsequently described as part of regional flora treatments (e.g. Hepper 1960; Hilliard & Burtt 1979; Philcox 1990). In his classification of *Alectra*, Melchior recognised two sections, one with two subsections, but this subdivision is not supported by phylogenetic analyses, hence they were not maintained in the latest infrageneric classification of the group (Morawetz 2007; Morawetz & Wolfe 2009).

Hitherto only one member of *Alectra* has been depicted in the present series, namely *A. orobanchoides*, but under its earlier name, *Melasma orobanchoides* (Phillips 1929). The morphological differences between *Alectra* and *Melasma* were clearly defined particularly by Melchior (1940), a distinction that subsequently has been supported by molecular evidence (Morawetz & Wolfe 2009). Four of the more obvious differences between the two genera are the presence in *Alectra* of flowers that are sessile or very shortly (< 5 mm) pedicellate (vs. pedicels 25–100 mm long), with the corolla marcescent (vs. shed after having faded), the calyx not inflating in fruit (vs. inflating), and the stigma strongly recurved, or 'horseshoe-shaped' and clavate (vs. nonrecurved clavate). In the classification of Morawetz (2007) the particular specimen illustrated in Phillips (1929) belongs to *A. orobanchoides* var. *orobanchoides*, one of the four varieties proposed for the species (voucher *Verdoorn 8019* in PRE).

Alectra orobanchoides has scale-like vegetative leaves and was described as holoparasitic by both Melchior (1941) and Morawetz (2007); it is also widely characterised as such in the literature. However, the plants do contain chloroplasts and chlorophyll (De la Harpe et al. 1981) and at times can be quite green, although this is often obscured by the abundant presence of purplish pigment (Hilliard & Burtt 1979; Visser 1981). Although capable of photosynthetic activity, the rate is quite low. Notwithstanding, the plant is demonstrably not holoparasitic. In *A. vogelii*, a species with well-developed leaves, the rate of photosynthesis is about half that of a host leaf on a per gram dry mass basis (Gouws et al. 1980). De la Harpe et al. (1981) established that *A. orobanchoides* is not able to fix carbon at a daily rate in excess of its diurnal requirements. With its much-reduced leaves, *A. orobanchoides*, like many if not most other hemiparasites, is at least partly dependant on its host for photosynthate. Despite such dependency, *A. orobanchoides* is best treated as a hemiparasite, a state that would then apply to the genus as a whole, including the atypical *Alectra fruticosa* from Madagascar, a sprawling shrub up to 1.5 m high that is morphologically intermediate between *Alectra* and *Melasma* (Fischer 1996; E. Fischer pers. comm.).

Alectra vogelii, the subject of the present contribution (Figures 1–4), is the most well-studied member of the genus because it is a parasitic agricultural weed of especially legume crops in many parts of sub-Saharan Africa (e.g. Rambakudzibga et al. 2002). Its taxonomy though, is still in need of more detailed study. The live plants illustrated here come from Kalkheuvel West near Broederstroom, located in the Cradle of Humankind World Heritage Site, South Africa, where they were associated with climax Highveld grassland on well-drained soil derived from dolomite (Figure 2a). When first encountered, the identity of the taxon was in doubt because in general appearance the plants looked different from many

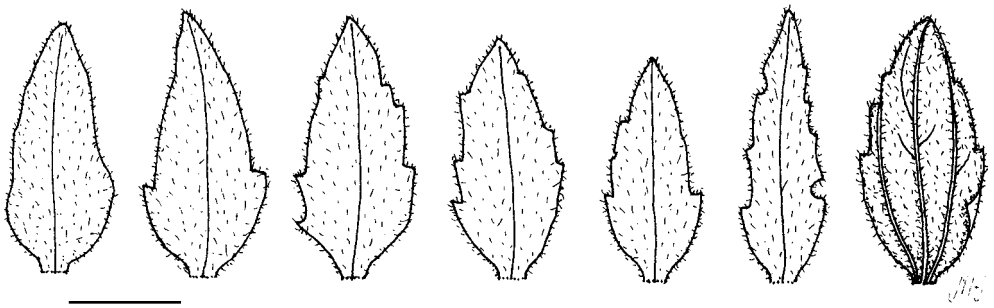

FIGURE 1.—Leaves showing a range of variation in shape and degree of margin dentation in a single stand of the form of *Alectra vogelii* figured in the plate (dorsal view, except far-right one which is in ventral view and depicting a tooth rolled-under). Scale bar: 15 mm. Artist: Jenny Hyde-Johnson.

published and online illustrations identified as *A. vogelii*. Moreover, *A. vogelii* is closely associated with cultivation and apparently is rarely found in undisturbed natural vegetation (Muasya 1996; CABI 2020). However, the material from Kalkheuvel West ran to this species in the identification keys of, amongst others, Melchior (1941), Philcox (1990) and Morawetz (2007), hence are here treated as such. At first glance these plants also appeared rather similar to the morphologically variable *A. sessiliflora*, the most widespread species within the genus (Morawetz & Wolfe 2011). The latter, however, has the lower bases of the anther thecae distinctly apiculate (Figure 4c), whereas those of *A. vogelii* are obtuse (Figures 4a, b). In *Alectra* this character of the anthers is of considerable taxonomic significance in being species-specific and constant.

Obtuse anther bases as in *Alectra vogelii* are, amongst others, also present in *A. capensis* and *A. orobanchoides*. These three species are closely related and form a separate clade within the phylogenetic tree of *Alectra* (Morawetz 2007; Morawetz & Wolfe 2009). *Alectra orobanchoides* is distinct in having the vegetative leaves reduced to scales; the stems, scales and calyces are green, usually variously flushed with purple. *Alectra capensis* is easily identified by having the largest flowers in the genus (corolla 28–30 mm long) and well-developed leaves that are elliptic to ovate, with the margins always entire. In *A. vogelii* the flowers are smaller (corolla (6–)8–15(–20) mm long) and the leaves well-developed with the margins entire or with 1–5 pairs of teeth (Figure 1).

Alectra vogelii was described by Bentham (1846: 339) from herbarium material collected in 1841 in Nigeria, near the confluence of the Niger and Benue rivers (Mount Patteh), by the German botanist, Julius Rudolph Theodor Vogel (1812–1841). The specific epithet honours Vogel, who at the time was the chief naturalist accompanying the ill-fated Niger Expedition of 1841, a venture backed by the British government (Allen & Thompson 1848; Hepper 1991). Of the 150 Europeans on the expedition, 42 died from fever (probably malaria), including Vogel (Hepper & Neate 1971).

In the taxonomic literature all species of *Alectra*, except *A. fruticosa*, are mostly described as annuals, an interpretation probably based on the behaviour of the better known *A. vogelii* under conditions of cultivation. As a weed of cultivation, certain forms of

FIGURE 2.—Habit and morphology of *Alectra vogelii* form in natural vegetation at Kalkheuvel West, South Africa: a, plant in flower, stems and leaves flushed with purple and parasitic on the grass, *Themeda triandra*; b, flowers, showing stamens, and style with clavate and recurved stigma; c, dug-up cluster of soil with orange-yellow stem and roots of the parasite, intermingled with grass roots. Scale bars: a, 20 mm; b, c, 5 mm. Photographs: a, c, J. Hyde-Johnson; b, A.E. van Wyk.

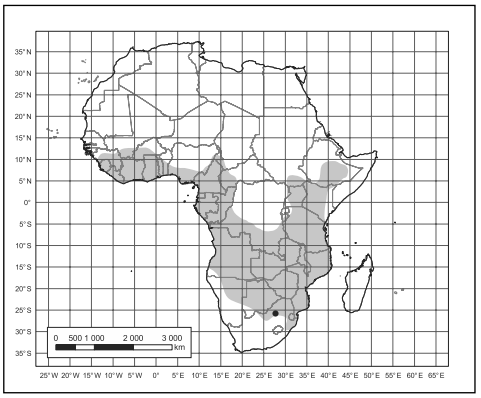

FIGURE 3.—Known distribution range of *Alectra vogelii* (shaded area) based on Morawetz (2007); distribution data kindly supplied by Prof. Eberhard Fischer, University of Koblenz-Landau, Germany; as well as specimens housed in the H.G.W.J. Schweickerdt Herbarium, University of Pretoria, and National Herbarium, Pretoria. Mostly recorded as a parasitic agricultural weed from cultivated fields. Black dot indicates locality of wild-growing plant figured in the plate.

A. vogelii parasitises annual crop plants and when its host reaches maturity, the parasite succumbs with it. But calling it an annual is misleading because in undisturbed natural vegetation *A. vogelii* (and at least all other species of *Alectra* in southern Africa) is mainly if not exclusively found on perennial hosts and clearly behaves as a perennial with annual aboveground shoots.

Field observations over a period of four years at Kalkheuvel West, have shown that the form of *Alectra vogelii* here figured parasitises perennial tussock grasses, notably *Themeda triandra* (Figure 2a). A particular stand of the parasite would annually emerge above ground in the same spot, usually in mid- to late summer (the rainy season) following an extended period of active growth by the host. The parasite seemingly proliferates underground and expands in clonal fashion with new sprouts appearing in the vicinity of mother plants. At this location we have never found the species as a parasite on one of the many legumes that are part of the rich flora of the area. Yet, as a weed of agriculture, the species mainly targets legumes, in particular cowpea (*Vigna unguiculata*), bambara groundnut (*Vigna subterranea*), peanut (*Arachis hypogaea*) and soybean (*Glycine max*), but also other types of beans and a few non-leguminous crop plants.

Given the wide geographical range of *Alectra vogelii* in sub-Saharan Africa (Figure 3), some infraspecific genetic, morphological and physiological variation might be expected. This is indeed the case with several geographical strains of this species examined, each showing differences in their virulence to parasitise various crop plants (Polniaszek & Parker 1987; Polniaszek et al. 1991). It is suggested that *A. vogelii* may well include several host-defined cryptic physiological races, some of which may be in a state of incipient speciation. This was, for example, shown to be the case in the hemiparasitic *Orobanche minor* (Thorogood et al. 2008, 2009). Further work should focus on reciprocal growth experiments on the various hosts and analysis of possible genetic divergence. Infraspecific variation in the morphology of plants is also reflected by the several names for morphological entities once proposed as separate infrageneric taxa, but which are now placed in synonymy under the species. Note, however, that the treatment of some taxa as synonyms of *A. vogellii* is in need of verification. For example, Engler (1922) described three new species of *Alectra*, namely *A. angustifolia*, *A. merkeri* and *A. scharensis*, but following examination of the type specimens these names were all placed in synonymy under *A. vogelii* by Melchior (1941), a view maintained by Morawetz (2007). However, neither explained the apparent discrepancy of such an association with *A. vogelii* when considering the original descriptions;

Engler clearly described the anthers of all three species as apiculate, whereas those of *A. vogelii* are obtuse. Did Engler really misinterpret the state of the anther thecae? Because of this uncertainty, we have not listed these names as synonyms in the synopsis above.

Our monitoring over four seasons of one particular stand/clone of *Alectra vogelii* at Kalheuvel West has revealed noticeable variation/plasticity in its time of flowering and the

FIGURE 4.—Morphology of stamens and anthers in *Alectra vogelii*, compared with *A. sessiliflora*: a, *A. vogelii*, stamens with anthers inverted, resulting in the bases of the thecae (whitish, obtuse, not apiculate, with slit-like pores) directed upwards towards mouth of flower; b, dried anther, as in an herbarium specimen (*Visser 243* in PRU) – note slit-like pore at theca base; c. *A. sessiliflora*, dried anther, as in herbarium specimen (*Van Wyk 3509* in PRU) – note widely opened thecae with distinctly apiculate bases. Scale bars: a, 1 mm; b, c, 100 μm. Photographs: A.E. van Wyk.

general appearance of the flowering shoots, three forms of which are figured in the plate (2376: 1, 2 & 3). Some flowering shoots were almost exclusively green, while adjacent ones had purple edges to the leaves and calyx lobes, whereas still other shoots were quite heavily flushed with purple. The appearance of purple has mainly been a late season development, but in 2020 some shoots turned purple very early, but then they only sprouted very late compared to previous years. We have assumed that the purplish colour is caused by anthocyanins. These pigments are known to accumulate in otherwise green photosynthetic tissue under certain stressful environmental conditions, such as drought and cold (Landi et al. 2015). However, in *A. vogelii* we could associate neither of these two conditions with the appearance of purple colouration. In 2017, a relatively wet season, many shoots had already changed to purple in February, whereas in a similarly wet 2020, this colour change happened much later in April. We speculate that variation in the exchange/availability of photosynthate and/or other compounds from the host may contribute towards the observed variation in purple pigmentation.

We could not find references to studies on the pollination biology of *Alectra* in general and *A. vogelii* in particular. In this connection the possible functional significance of the two different types of anthers in the genus remains to be elucidated. Observations on herbarium material of *A. sessiliflora*, a species with apiculate anthers, showed that each theca opens by means of a longitudinal slit, the margins of which then part sideways to fully expose the pollen content (Figure 4c). On the other hand, in *A. vogelii*, with obtuse anthers, the thecae in the fresh flowers of the Kalheuvel West plants only open by means of a slit-like pore at the theca base (Figures 4a, b). The theca bases also have a whitish colour compared to the greyish green, greenish yellow or yellow of the rest of the anther. However, it remains to be established in live plants if this opening mechanism applies to the species as a whole. In herbarium material investigated from elsewhere in Africa, the anthers in many instances do show thecae with a longitudinal slit, but the edges of the slit remain more or less appressed and only spread slightly at the base to form a pore-like slit. It is not clear if these longitudinal slits were already present in live plants, or were introduced as a result of desiccation during the preparation of the herbarium specimens. In the live material studied the stamens were more or less connivent with the anthers inverted on the filaments, resulting in the anther pores being directed towards the mouth of the flowers (Figure 4a). This configuration is reminiscent of the anthers in flowers adapted for buzz (vibratile) pollination (Buchmann 1983; Vallejo-Marín 2019), a possibility in need of further investigation.

The only observations of potential pollinators of *Alectra vogelii* plants at Kalkheuvel West were two unidentified species of bee fly (Diptera: Bombyliidae). We did, however, record a few other insect associates. All aboveground parts of the plants were destructively fed on by a hairy black caterpillar, larva of the moth, *Radiarctia lutescens* (Lepidoptera: Arctiinae: Erebidae) (Figure 5a). A small unidentified bagworm (Lepidoptera: Tineoidea: Psychidae), with a case constructed out of silk and sections of grass culm, preferentially fed on the developing capsules and were particularly abundant in some years (Figure 5b). Amongst the sap-sucking insects were an unidentified green shield bug (Hemiptera: Pentatomidae) and both the nymphs and adults of the tropiduchid planthopper, *Johannesburgia rossi* (Hemiptera: Tropiduchidae) (Figures 5c, d). The adult planthoppers showed a particular preference for feeding on the flower buds.

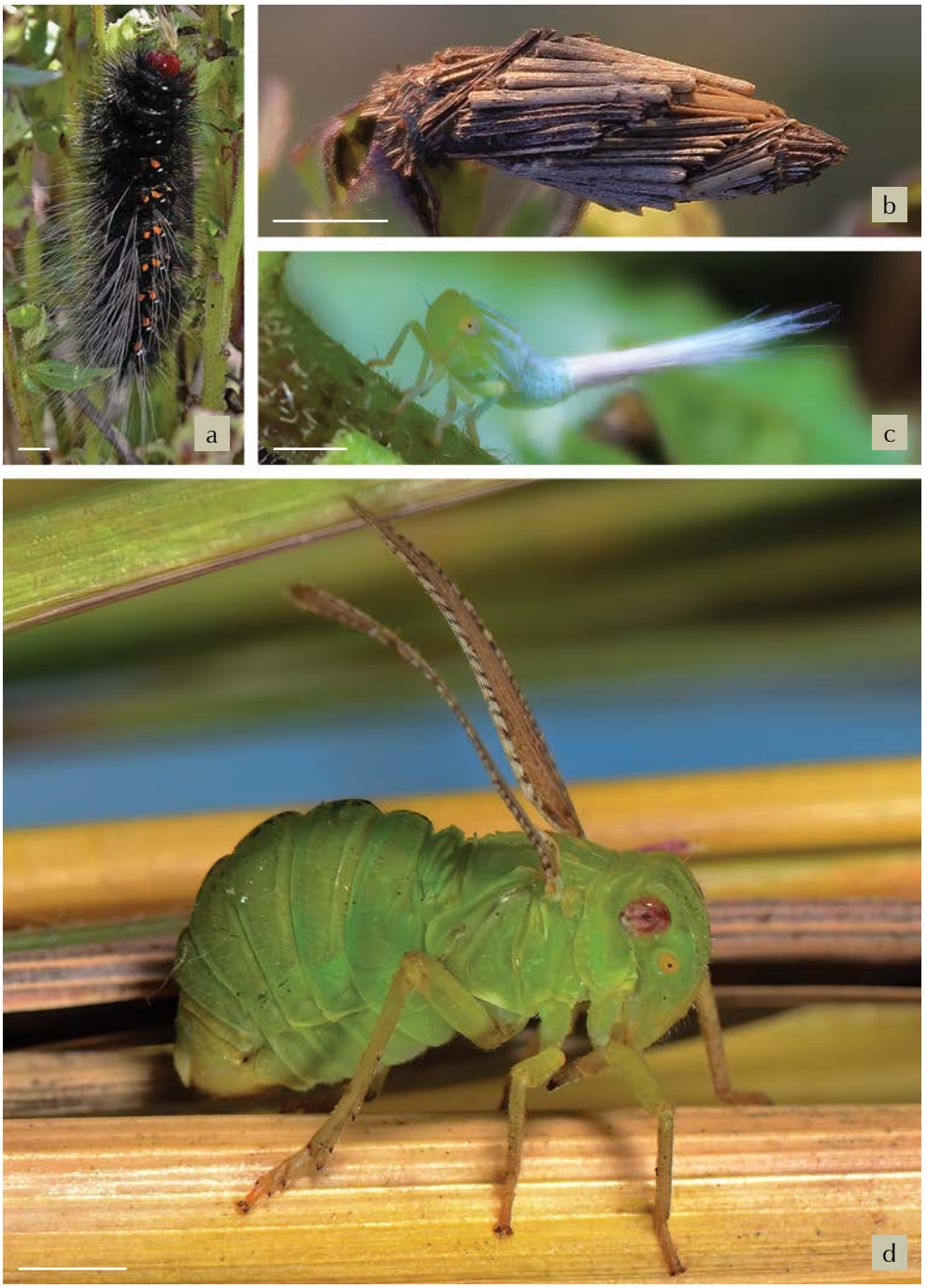

FIGURE 5.—Insects associated with the form of *Alectra vogelii* at Kalkheuvel West: a, caterpillar of the moth, *Radiarctia lutescens*; b, unidentified bagworm (Lepidoptera: Tineoidea: Psychidae); c, d, two life stages of the tropiduchid planthopper, *Johannesburgia rossi*, nymph (c) and adult insect (d). Scale bars: a, 3 mm; b, 5 mm; c, 2 mm; d, 1 mm. Photographs: a–c, J. Hyde-Johnson; d, P. Webb.

As discussed above, *Alectra vogelii* is well known as an agricultural weed. Its weediness has been studied extensively. A detailed review of these mostly agronomical and plant physiological aspects of the species would fall outside the scope of the present contribution, hence only the following brief comments must suffice. Although reported as a parasitic weed on mainly susceptible legume crop cultivars throughout its range, the greatest impact is in low-input subsistence farming systems, and especially ones involving cowpea (Alonge et al. 2001a, b; Rambakudzibga et al. 2002; Rugare et al. 2013). A useful online overview of the agricultural importance of *A. vogelii* is provided by the Invasive Species Compendium of the Centre for Agriculture and Bioscience International (CABI 2020). The extremely small seeds are produced in great profusion, with about two million of them making up one gram (Visser 1978). The seeds can, according to anecdotal evidence, remain dormant in the soil for up to 12 years (Parker & Riches 1993). Seeds will only germinate in response to chemical stimulants produced by the roots of other plants (Botha 1948; Visser 1978). Contact between parasite and host is quickly established, the finer points of which have been described in much detail (e.g. Dörr et al. 1977, 1979; Visser et al. 1977). Resistance to parasitic plants may occur at different stages of the parasitic life cycle, often after initial contact with a potential host. In the case of less compatible legume host species, penetration by *A. vogelii* generally stopped in the host cortex, possibly due to an inability of the penetrating parasitic cells to digest the host cell walls (Visser et al. 1990). Such plant–plant resistance involves several molecular mechanisms and signalling pathways (Yoder & Scholes 2010). Photosynthesis and the exchange of photosynthate between parasite and host were studied by Gouws et al. (1980). Strategies for the management of *A. vogelii* and other parasitic weeds in legume crops were reviewed by Rubiales & Fernández-Aparicio (2012).

Considering its wide distribution in sub-Saharan Africa (Figure 3), surprisingly few vernacular names and biocultural uses have been recorded for *Alectra vogelii*. This also applies to the African members of the genus in general. In the case of *A. vogelii*, *A. sessiliflora* and most probably also other species, the orange-yellow underground roots and stems (Figure 2c) were formerly used in southern Africa as a source of pigment (see further on) to dye textiles and leather (WAT 1926; Van Wyk & Gericke 2018), and in the Democratic Republic of the Congo (DRC), wood (Jansen 2005). The Afrikaans name *verfblommetjie* ('paint flower'), for an *Alectra* in general, refers to this particular use. The preferred English name for *A. vogelii* is yellow witchweed. Other names for it include cowpea witchweed and Vogel alectra; *geelblom* and *vogel-alectra* (Afrikaans); *matebelwê* (Tswana); *onime* (Wambo); *bumbulani*, *kiri nsi* and *tchimfele patta galonga* (all three from DRC; source languages not recorded) (Troupin 1949; Rodin 1985; Cole 1995).

Unlike the situation in Africa, one specific member of *Alectra* is greatly valued as a medicinal plant in India. Long referred to as either *A. parasitica*, *A. chitrakutensis* or *A. parasitica* var. *chitrakutensis*, this taxon is treated as *A. orobanchoides* var. *parasitica* in Morawetz's (2007) monograph. It is considered a rare plant and is parasitic on the roots of the tree *Vitex negundo* (Lamiaceae), itself widely used in folk medicine. This *Alectra* has been employed for centuries in traditional Ayurvedic medicine for the treatment of, amongst others, leprosy, tuberculosis, paralysis, swellings, fever, intestinal worms and constipation (Kakpure & Rothe 2012; Sharma et al. 2016). One of the pharmacologically active compounds isolated from the taxon is azafrin, the pigment responsible for the characteristic orange-yellow colour of the underground parts in most members of *Alectra*, including

A. vogelii (Agrawal et al. 2014; Patil 2020) (Figure 2c). Azafrin is a natural carotenoid acid (C_{27}-apocarotenoid) with a limited distribution in a few higher plants and lichens (Eugster 1979; Moise et al. 2014). This compound exhibits antioxidant activity and shows promise as a cardioprotective adjuvant for the prevention and/or treatment of cardiovascular disease, in particular those related to myocardial ischemia (Yang et al. 2018).

Description.—Annual or perennial (depending on duration of host) hemiparasitic herb (120–)200–300(–500) mm tall, parasitic on roots of other herbs, especially grasses and legumes, most often recorded as a weed of cultivation; individual plants may proliferate vegetatively underground (especially when on a perennial host) resulting in a clone of separate aboveground shoots. *Stems* erect, simple or branched, terete to angular, pilose to hispid, green, sometimes variously flushed with pink or purple; base of stems and roots orange-yellow. *Leaves* opposite, becoming subopposite or alternate within inflorescence, narrowly ovate to lanceolate, (7–)20–30(–40) × (3–)8–15(–20) mm, green or variously flushed with purple, 3–5-veined, hispid to subglabrate; base cuneate; apex acute to rounded; margin entire or with 1–5 pairs of blunt or sharp teeth, plane or rolled-under, especially some of the teeth and/or towards the tip; petiole 1–3 mm long. *Inflorescence* a dense to loose terminal raceme; flowers solitary in axils of upper leaves or leaf-like bracts; bracts linear to lanceolate or narrowly ovate, 8–20(–25) × 2–5 mm, margin entire or with 1 or 2 pairs of blunt or sharp teeth, base cuneate to attenuate, apex acute to rounded, green or variously flushed with purple, especially along the margin, subglabrate to hispid; petiole 1.0–2.5 mm long; bracteoles 2, linear, 3.5–10.0 × 0.5–2.0 mm, hispid to subglabrous; pedicels (2–)5–8 mm long. *Calyx* campanulate, 5-lobed, (5–)10–15 mm long, hispid to subglabrate; lobes triangular, 3–6 × 2.5–6.0 mm, apex acute to obtuse, margin ciliate. *Corolla* campanulate, 5-lobed, golden yellow with each lobe 3-veined, venation sometimes bright red on dorsal surface, (6–)8–15(–20) mm long, glabrous or subglabrate, soon withering but persistent in calyx and remaining over the capsule; lobes 5–10 × 4–10 mm, rounded. *Stamens* 4, inserted below the middle of the corolla, included, slightly unequal, the longer pair 3.5–12.0 mm long, the shorter pair 2.5–10.0 mm long; filaments all glabrous or with a few scattered hairs, especially distally; anthers ± 1.5 × 0.5 mm, inverted, thecae often slightly unequal in length, greyish green, greenish yellow or yellow but whitish at the base, each theca opening at the base with a slit-like pore (in live material of wild-growing form investigated in the present study), in herbarium material some thecae seemed to have opened by means of a longitudinal slit (due to desiccation?), although the edges of the latter tend to stay appressed over most of their length, only to part noticeably towards the base to form a pore-like slit, base acute to rounded, not apiculate. *Ovary* ovoid, 1.5–4.0 × 2–4 mm, glabrous. *Style* 3–13 mm long; stigma clavate, recurved. *Capsule* broadly ovoid to globose, 5–10 × 4–8 mm, loculicidally dehiscent. *Seeds* numerous, linear or clavate, ± 1 × 0.25–0.30 mm, translucent green, surface of seed coat reticulate due to shallow indentations. *Chromosome number*: $2n = 38$ (Dörr et al. 1977). Plate 2376.

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Thunbergia battiscombei Acanthaceae

Democratic Republic of the Congo, Ethiopia, Kenya, South Sudan, Uganda

Thunbergia battiscombei *Turrill* in Hooker's Icones Plantarum 31: t. 3041 (1922); Andrews: 191 (1956); Turrill: t. 383 (1962); Schönenberger: 23, 24 (1999); Hedberg et al.: 349 (2006); Vollesen: 59 (2008); Darbyshire et al.: 8 (2015). *Thunbergia adjumaensis* De Wildeman: 419 (1928).

The genus *Thunbergia* Retz., which includes the well-known black-eyed susan (*Thunbergia alata* Bojer ex Sims) and Bengal clock-vine (*Thunbergia grandiflora* (Roxb. ex Rottler) Roxb.), contains ± 102 species (The Plant List 2005; African Plants Database 2012). Growth forms of members in the genus are variable and include erect, trailing or twining annual or perennial herbs, scandent shrubs or woody twiners, and all species are without cystoliths (calcium oxalate crystals) (Marloth 1932; Leistner 2000; Vollesen 2008; Hyde et al. 2018).

Lawrence Montin (1723–1785), a distinguished pupil of Linnaeus and honoured in the genus name *Montinia* Thunb. (Montiniaceae), described *Thunbergia* Montin in 1773 as a genus in the Rubiaceae (coffee family). In 1780, Ander John Retzius (1742–1821) used the genus name *Thunbergia* to describe plants of Acanthaceae (acanthus family) collected by Thunberg in the Cape, South Africa. This made *Thunbergia* Retz. a later homonym and therefore an illegitimate name, leading the younger Linnaeus, denoted as L.f., to disregard it in 1781. Authors like Lindau (1893) and Clarke (1912) associated the genus *Thunbergia* with L.f. This is because he cited '*Thunbergia capensis* Montin' as a synonym (instead of *Thunbergia* Montin) when he described *Gardenia thunbergia* L.f., the first South African gardenia introduced in 1773 to the Kew Gardens by Sir James Cockburn Bart (Sims 1807). Almost 200 years later, the authorship of the genus was resolved through conservation of *Thunbergia* Retz., based on *T. capensis* Retz. as the type species. Montin's *Thunbergia* is a synonym of the genus *Gardenia* J.Ellis in the family Rubiaceae.

Retzius named the genus *Thunbergia* (Retzius 1780) in honour of Linnaeus' student, Carl Peter Thunberg (1743–1828), a Swedish physician and botanist employed by the Dutch East India Company (Nordenstam 1994). Thunberg travelled to Asia and the East Indies and visited South Africa (Cape of Good Hope) during 1772–1775 where he collected plant specimens, among them *T. capensis* Retz., which he sent to Linnaeus (Retief & Reyneke 1984). Through the specimens that he collected in the Cape of Good Hope region from 1772 to 1774 (Aitken 2007), he became known as the 'father of South African botany' (Gunn & Codd 1981; Nordenstam 1994). During his three years in the Cape, Thunberg learnt Dutch, which afforded him the opportunity to go to Japan via the Dutch East Indian Company, to serve as a physician (and botanist), as only the Dutch were allowed entrance to Japan at that time (Gunn & Codd 1981). Through his botanical work in Japan he also became known as the 'Japanese Linnaeus', and eventually returned to Sweden in 1779 to ultimately succeed Linnaeus as Professor of Botany at Uppsala University (Gunn & Codd 1981).

PLATE 2377.—1, leafy twig, × 1; 2, flowering branch, × 1. Voucher specimen ex hort: *Condy 288* in National Herbarium, Pretoria. Artist: Gillian Condy.

PLATE 2377 *Thunbergia battiscombei*

The Acanthaceae includes three subfamilies namely Acanthoideae (containing most of the species), Nelsonioideae and Thunbergioideae s.l. (Scotland & Vollesen 2000). The Thunbergioideae has ± 170 species in five genera, the largest being *Thunbergia*, followed by *Mendoncia* Vell. ex Vand. (± 60 species) and *Pseudocalyx* Radlk. (± 7 species) while the two remaining genera, *Anomacanthus* R.D.Good and *Meyenia* Nees have one species each (monotypic). Members of the subfamily are recognised by their mostly twining habit (erect in some *Thunbergia* species), large floral bracteoles, reduced calyx, lack of endothecia and absence of cystoliths (Schönenberger 1999). The absence of cystoliths is conspicuous, since Steyn & Condy (2019) provided a summary of characters for distinguishing the Acanthaceae, and among these 'decussate leaves with cystoliths' are usually present in the family. The fruit in Thunbergioideae are either dry and dehiscent capsules without retinacula (*Thunbergia*, *Pseudocalyx*, *Meyenia*) or fleshy drupes (*Mendoncia*, *Anomacanthus*) and differ from the Acanthoideae where the capsules are equipped with retinacula serving as levers to eject seeds from capsules somewhat explosively (Borg et al. 2008).

The flowers of *Thunbergia* are large and attractive compared to other genera in Thunbergioideae and many other Acanthaceae (Schönenberger 1999). Furthermore, fruiting capsules in the genus are round with long, tapered beaks (Retief & Reyneke 1984). Apart from growth form, Hyde et al. (2018) reported two other characters to help distinguish *Thunbergia* from other genera in the Acanthaceae, namely their calyx type with numerous lobes and their anther dehiscence. Borg et al. (2008) surmised habit (growth form), calyx morphology and anther dehiscence patterns appear to reflect molecular evolutionary relationships especially well among *Thunbergia* species, while anther appendages and stigma structure are fairly unstable and most likely associated with differences in pollination biology.

A comparative study of the floral structure and development of 18 species of *Thunbergia* was carried out by Schönenberger (1999). His study concurred with Clarke (1912) in that the flowers of *Thunbergia* are greatly diversified and show a broad range of evolutionary adaptations for pollination. While there is high diversity in the flowers at anthesis, there is uniformity during the early developmental stages. For example, in all species investigated by Schönenberger (1999), the calyx arose as a ring primordium; the corolla is 'late sympetalous', i.e. the floral apex widens and the petals fuse via interprimordial growth behind the stamens; and petals and stamens are initiated more or less simultaneously. Furthermore, the genus shows a wide spectrum of insect and bird pollination syndromes (Schönenberger 1999). *Thunbergia* species are visited by insects such as the moth, *Filodes costivitralis* Guenée (Hyde et al. 2018).

Thunbergia is distributed predominantly in the tropics and subtropics of the Old World (Schönenberger 1999; Borg et al. 2005), while some species are now naturalised in the New World tropics (Deng et al. 2011). According to Bremekamp (1955), there are 46 *Thunbergia* species in the Malesian region (Malaysia, Indonesia, New Guinea, the Philippines and Brunei). Elsewhere, four species are recognised in Australia (Barker 1986), six species in China (Deng et al. 2011) and ten in India (Santapau & Henry 1973), but the region with the most diversity is Africa (tropical and subtropical) with 49 species recorded by Vollesen (2008), 11 of which are found in southern Africa (Retief & Reyneke 1984).

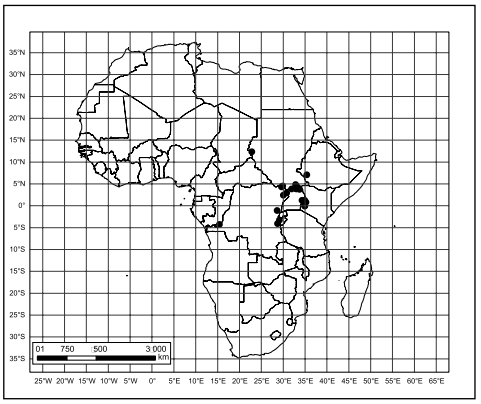

FIGURE 1.—Known geographical distribution of *Thunbergia battiscombei* in Africa based on data from the Global Biodiversity Information Facility (www.gbif.org), Turrill (1962) and Vollesen (2008).

Species of *Thunbergia* have been reported to have a number of uses. According to Teron (2005), the Karbi people of India regard *T. grandiflora* as a sacred plant using it to nullify evil influences during worship. They also use it to cure minor eye sore and, in combination with other plants, to treat snakebite (Teron 2005). Leaves of *T. grandiflora* are used as a vegetable (Patiri & Borah 2007). They are also used against stomach ailments (Sarma 2006), while the roots are used to treat toothache and bone fractures (Sarma 2006). Roots of *Thunbergia coccinea* Wall. ex D.Don, on the other hand, are used in the treatment of dysentery, stomach ache and fever (Sarma 2006), while fresh root extracts are used as a health tonic and aphrodisiac (Kar et al. 2013). *Thunbergia alata* is traditionally planted in gardens as an ornamental, and *T. erecta* T.Anderson roots are reportedly used in traditional medicine to treat patients with psychiatric disorders (Kar et al. 2013). However, reports on uses of other *Thunbergia* species are limited.

Thunbergia battiscombei, commonly known as scrambling clock-vine (Neal 2012), is an African species that is distributed through the Democratic Republic of Congo, Ethiopia, Kenya, South Sudan and Uganda (Vollesen 2008) (Figure 1). This species was named after Edward Battiscombe (1874–1971), who collected the type species (Turrill 1962). He was an author, plant collector and forest conservationist for the British East African Protectorate in the 20th century. The floral morphology of *T. battiscombei* is similar to that of *T. petersiana* Lindau; however, it differs in that the calyx is hairy and the sepal lobes and teeth are relatively large (Schönenberger 1999). According to Turrill (1962), the species occupies a broad range of habitats in Kenya and Uganda, which has given rise to a variety of growth habits, including erect or twining herbs and creepers. *Thunbergia battiscombei* is found growing at altitudes of 750–2 300 m above sea level in broad-leaved woodland (especially *Combretum* woodland), grassland that is prone to annual fires, riverine thicket (Vollesen 2008), rocky hillside (Turrill 1962) and is also cultivated across its natural range as an ornamental plant (Darbyshire et al. 2015). In Uganda, it occurs in West Madi, Metu and Anua River of the West Nile District; on the Imatong Mountains and Mount Lomwaga in the Acholi District; and near Mbale in the Mbale District (Vollesen 2008). In Kenya, it has been recorded in the Nyanza basin (Turrill 1922) and on the foothills of Mount Elgon in Trans Nzoia District and Soy in Uasin Gishu District (Vollesen 2008).

According to Turrill (1962), leaves of *Thunbergia battiscombei* are used as a covering by women in Africa. Amongst gardeners, our species and other thunbergias are a favourite because of their large, attractive flowers (Figure 2) and tolerance to a range of soil conditions. The species responds well to application of fertiliser by regular bouts of flowering (Scheper 2005). While the plants grow in sunny areas, they can also survive in total shade, but with fewer flowers produced (Scheper 2005). Water must be provided when the soil

FIGURE 2.—*Thunbergia battiscombei* at Petal Faire Nursery, Pretoria: a, floriferous in garden bed; b, side view of flowers showing cream-yellow tube; c, front view of flowers and buds. Photographs: L. Williams.

is dry, especially when grown in full sun. Nonetheless, they will survive short periods of drought (Scheper 2005). Plants may be damaged by frost but grow back in the spring.

Thunbergia battiscombei is propagated by stem cuttings in summer or by seed harvested in late winter to early spring (Neal 2012). Plants growing in Florida, USA, do not produce seed, possibly because the pollinators are absent (Scheper 2005). The sprawling stems also make natural layers where they touch the ground, forming clumps that can be dug up and divided. *Thunbergia battiscombei* can be used as a large shrub in the landscape if left to spread at the back of a flower bed (Scheper 2005). They can also be grown on a trellis or relatively large container plant (Neal 2012). When grown in a hanging basket, the gold-throated, blue-purple flowers provide a grand show at eye-level. This species is complimented well in the garden with other tropical plants like begonia and impatiens and thrives in any type of container garden (Scheper 2005).

As a species with very attractive flowers, *Thunbergia battiscombei* has caught the eye of field workers and botanical artists alike, including Matilda Smith (1854–1926), Margaret Stones (1920–2018) and Gillian Condy (1952–). Matilda Smith's botanical artistry was featured in Curtis's Botanical Magazine (2 300 plates; Sampson 1985) for more than 40 years (Ogilvie & Harvey 2003). She was the first artist to paint in-depth illustrations of the New Zealand flora; became the first official artist at the Royal Botanic Gardens, Kew, and she was the second elected female associate member of the Linnaean Society of London (Sampson 1985). Incidentally, she was the second cousin of J.D. Hooker and was responsible for about 1 500 plates in Hooker's Icones Plantarum, with plate 3041 being a line drawing of *T. battiscombei*. Margaret Stones painted *T. battiscombei* in 1962 (Turrill 1962) while working as a freelance artist, later becoming principal contributing artist for Curtis's Botanical Magazine, where she ultimately illustrated about 400 plates over 24 years (Chance & Morgan 1990; Smyth 2010). She went on to become the illustrator in six volumes of *The Endemic Flora of Tasmania* (Smyth 2010) and was responsible for 200 drawings in *Native Flora of Louisiana*, a project she was involved in for about 10 years (Chance & Morgan 1990). Louisiana State University owns numerous original drawings (pencil, pen-and-ink and colour plates) of Margaret Stones, which she produced for *Curtis's Botanical Magazine* (Chance & Morgan 1990). Gillian Condy, who illustrated the accompanying plate (Plate 2377) for this contribution, is a Nairobi-born, South African who has illustrated over 400 plates for *Flowering Plants of Africa*. Prior to her retirement, she was the resident botanical artist at the National Herbarium in Pretoria, South Africa for more than 30 years (Best 2016). Among a long list of achievements, Condy was the recipient of a gold medal from the Royal Horticultural Society (Best 2016). She was also chosen to illustrate a cultivated colour form of *Strelitzia reginae* 'Mandela's Gold', which she had the privilege of presenting to Nelson Mandela in person (Best 2016).

Description.—Evergreen shrub or perennial herb with a woody rootstock; stems erect, up to 750 mm tall (rarely twining to 3 m long). *Leaves* slightly fleshy, palmately veined; petiole 10–40 mm long, smooth surface or thinly dispersed hairs usually with lines of hairs at nodes; lamina ovate to elliptic or slightly obovate, largest 55–95 mm long; apex slightly tapering to broadly rounded, ending abruptly with a sharp tip; base attenuate to appearing as if cut off, decurrent, margin entire or with a few large irregular teeth. *Inflorescence* numerously flowered axillary racemes (2 racemes per axil or 1 raceme and a solitary flower are rare); each flower clasped by 2 large ovate to elliptic bracteoles up to 27 mm long,

glabrous to finely puberulous. *Bracts* caducous, lower foliaceous, upper bracteole-like; pedicels 8–35 mm long, puberulous. *Bracteoles* pale green with conspicuously raised dark-green reticulation, ovate to elliptic, 20–27 × 8–12 mm, acute to obtuse, apiculate, puberulous. *Calyx* puberulous, 2–4 mm long of which the broadly triangular lobes are about half its length. *Corolla* limb and upper part of tube purple to royal blue, lower part of tube whitish, throat yellow; tube 30–45 mm long; lobes 10–20 mm long. *Stamens* in fours, included in throat; filaments 10–15 mm long, glabrous; anthers with 2 thecae, 1 with a long curved spur, 2–3 mm long. *Capsule* 8–10 mm in diameter, beak 16–20 mm long. *Seeds* pale brown, ± 7 mm in diameter with reticulate surface and strong lateral ridge. *Flowering time*: from late spring to early autumn. Plate 2377.

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PLATE 2378 *Justicia divaricata*

Justicia divaricata Acanthaceae

Angola, Botswana, Mozambique, Namibia, South Africa, Eswatini, Zambia, Zimbabwe

Justicia divaricata *Licht. ex Roem. & Schult.* in Systema vegetabilium 1: 163 (1817); Dietrich: 211 (1818); Anderson: 42 (1864) [as '(Nees) T. Anderson']; Vollesen: 216 (2015) [as '(Nees) T. Anderson']; Van Rooyen & Van Rooyen: 92 (2019). *Gendarussa incana* Nees var. *villosa* Nees: 367 (1841). *Adhatoda divaricata* Nees: 391 (1847). *Adhatoda capensis* (Thunb.) Nees var. *arenosa* Nees: 391 (1847); *Justicia mossamedea* S.Moore: 312 (1880). *Justicia nepeta* S.Moore: 312 (1880). *Justicia namaensis* Schinz: 202 (1890); *Justicia divaricata* (Nees) T.Anderson: 42 (1864) 'nom. superfl.'. *Monechma floridum* C.B.Clarke: 219 (1900). *Monechma nepeta* (S.Moore) C.B.Clarke: 219 (1900). *Monechma spissum* C.B.Clarke: 219 (1900). *Monechma fimbriatum* C.B.Clarke: 72 (1901). *Monechma divaricatum* (Licht. ex Roem. & Schult.) C.B.Clarke: 72 (1901) [as '(Nees) C.B.Clarke']; *Monechma nepetoides* C.B.Clarke: 73 (1901). *Monechma namaense* (Schinz) C.B.Clarke: 73 (1901). *Monechma angustissimum* S.Moore: 137 (1903). *Monechma eremum* S.Moore: 231 (1907). *Monechma terminale* S.Moore: 75 (1908).

TYPE.— [South Africa, Northern Cape], Grootrivierspoort prope fluvium tkaigarieb s. Oranjerivier ad montes, [1805], *Lichtenstein s.n.* (No. 355 in Herb. WILLD) (holotype B-W 00355 -01 0, scan!).

The Acanthaceae are an angiosperm family of about 220 genera and over 4 500 species in the order Lamiales (APG IV) (Heywood et al. 2007; Mabberley 2008; Vollesen 2008, 2013). Members of the family are mostly represented by annual and perennial herbs, shrubs and climbers, with relatively few trees (Darbyshire & Luke 2016). The family is mainly distributed in tropical and subtropical regions of the world and is seldom found in temperate areas (Heywood et al. 2007; Vollesen 2008, 2013). The highest diversity within southern Africa is found in the northeastern parts of the region with relatively high summer rainfall (Koekemoer et al. 2013; SANBI 2020). Acanthaceae are one of the 20 largest plant families in southern Africa, represented by ca. 40 genera and 379 species (SANBI 2020). Subfamilial relationships within the Acanthaceae have been problematic since Lindau's (1895) classification. According to Stevens (2001 onwards) the family is divided into four subfamilies with subfamily Acanthoideae divided into six tribes. The tribe Justicieae (subfamily Acanthoideae) is the most taxonomically difficult group in the family (Kiel et al. 2017) with tricolporate hexapseudocolpate pollen a synapomorphy for the group.

According to Van Wyk & Gericke (2000) and Awan et al. (2014), many members of Acanthaceae contain compounds with anti-fungal, cytotoxic, anti-inflammatory, insecticidal or anti-viral activity. In southern and eastern Africa, the family has a variety of medicinal uses including treatment for coughs, diarrhoea, fevers, toothache, infertility, muscular pains, and antidotes for snakebite (Watt & Breyer-Brandwijk 1962; Van Wyk & Gericke 2000). The Acanthaceae are an ecologically important plant family in sub-Saharan Africa (Kroon 1999; Vollesen 2000; Wahlberg 2001; Darbyshire et al. 2020) as it provides important

PLATE 2378.—1, flowering stem, × 0.75; 2, corolla, × 2; 3, capsule, × 2. Voucher specimen: *Condy 346* in National Herbarium, Pretoria. Artist: Gillian Condy.

ecosystem services and are of economic importance as fodder for livestock and wildlife (Vollesen 2000; Mannheimer et al. 2008; Tripp et al. 2017; Darbyshire et al. 2019b).

The genus *Justicia* (tribe Justicieae) was named after James Justice (1698–1763), a Scottish horticulturist (Munday 1995). The circumscription of the genus has historically followed one of two divergent trends – the adoption of a broad view of the genus, or the recognition of smaller, relatively homogenous segregate genera (Manning & Goldblatt 2014; Kiel et al. 2017). Graham (1988) retained *Monechma* Hochst. as distinct from *Justicia* based on its two-seeded capsules containing smooth, compressed seeds; whereas, *Justicia* was characterised by having mainly four-seeded capsules containing weakly compressed, mostly rugose (rarely smooth) seeds (Clarke 1901; Balkwill & Immelman 1995; Manning & Goldblatt 2014). The currently accepted circumscription of *Justicia* (Stevens 2001; Vollesen 2010, 2015; Manning & Goldblatt 2014; Kew 2020) includes well-established genera like *Adhatoda* Miller, *Aulojusticia* Lindau, *Duvernoia* E.Mey. ex Nees, *Monechma* and *Siphonoglossa* Oersted. Recent molecular phylogenetic studies on *Justicia* and related genera, however, have demonstrated that *Justicia* s.l. is paraphyletic with several major, morphological distinct lineages embedded within it (Kiel et al. 2017). Instead of treating the entire Justicioid lineage (Kiel et al. 2017) as a single genus as currently the case, an alternative would be to subdivide *Justicia* s.l. into a number of segregate genera (Darbyshire et al. 2019a, 2020). Therefore, several *Justicia* species, including *J. divaricata,* may undergo a name change in future.

Justicia s.l. is the largest genus in the family Acanthaceae and is estimated at about 600–700 species worldwide (Graham 1988; Vollesen 2010, 2015; Manning & Goldblatt 2014) with ca. 53 species indigenous to southern Africa (SANBI 2020). The southern African members of the genus are placed in eight sections mainly based on the structure of the inflorescences, the number of seeds per locule and pollen characteristics (Manning & Goldblatt 2014). Many species of *Justicia* are described as being heavily browsed and the roots of *J. odora* are used by the Zulus to make scented beads (Munday 1995). *Justicia capensis* is traditionally used to attract customers or improve chances of employment (Viljoen 2008), while several species are cultivated as garden ornamentals.

Justicia divaricata, currently included in section *Monechma*, formerly included in the genus *Monechma*, is a monophyletic species, albeit with significant phylogenetic diversity, confirmed by its long list of synonyms. It occurs widely in southern Africa and is commonly known as wild lucerne; *wilde lusern* or *maklikbreek* (Afrikaans) and is favoured by game and livestock (Munday 1980). *Justicia divaricata* is easy to distinguish from the rest of *Justicia* sect. *Monechma* and from most other members of *Justicia* s.l. through the absence of a fifth calyx lobe, and each lobe with a distinctive green midstripe with pale margins. *Justicia divaricata* differs from *J. minima* (section *Tyloglossa*), the only other member of the genus with a four-lobed calyx occurring in southern Africa, in having a two-seeded capsule (vs. four-seeded capsule) with seeds glabrous, ± flat on one surface and curved and somewhat ridged centrally on the other side (Darbyshire et al. 2020) (vs. seeds tuberculate, ovate to elliptic).

The oldest known specimen of *Justicia divaricata* is the one housed in the herbarium of the Botanic Garden and Botanical Museum Berlin-Dahlem (B) (Vollesen 2015) (Figure 1). This specimen was almost certainly collected by Martin Hinrich Carl Lichtenstein

FIGURE 1.—Scanned image of holotype of *Justicia divaricata* Licht. ex Roem. & Schult. (*Lichtenstein s.n.*, B -W 00355 -01 0). Curators Herbarium B (2000+). Digital specimen images at the Herbarium Berolinense. [Dataset]. Version: 06 Apr 2020. Data Publisher: Botanic Garden and Botanical Museum Berlin. http://ww2.bgbm.org/herbarium/ [https://herbarium.bgbm.org/object/BW00355010, image ID: 237139].

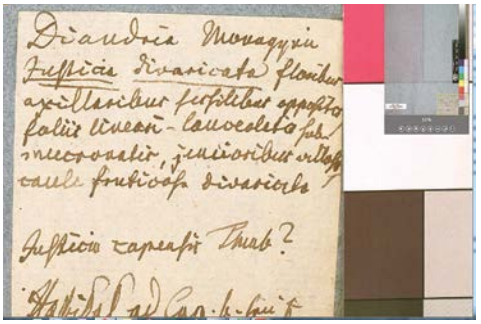
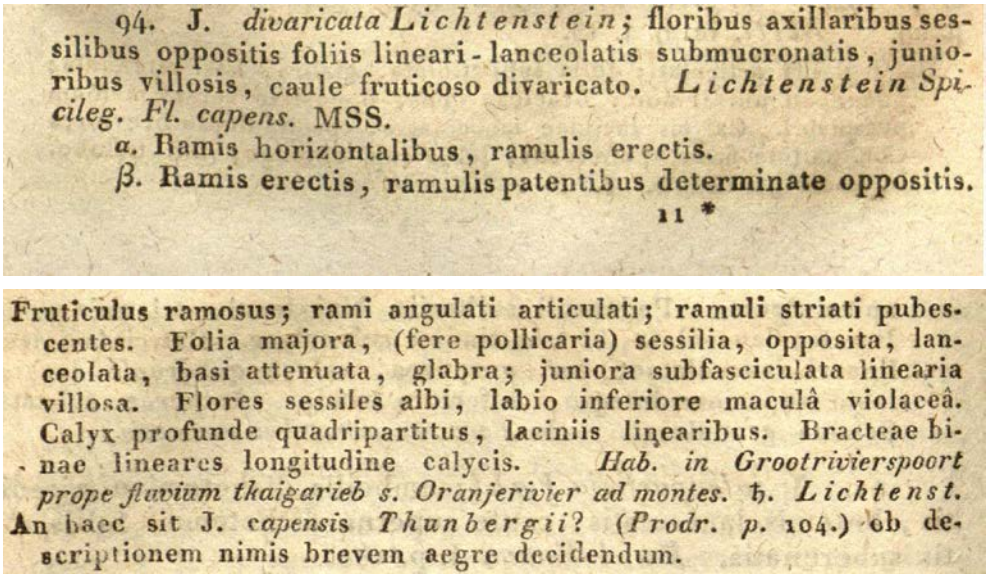


FIGURE 2.—Willdenow's handwritten description of *Justicia divaricata* as seen in Herbarium Berolinense (B).

(1780–1857) in 1805 and not by Count von Hoffmannsegg as indicated in Vollesen (2015). Lichtenstein arrived in Cape Town on 23 December 1802 as a German tutor to the son of the newly appointed Dutch Governor, General Jan Willem Janssens and took part in five expeditions into the interior of South Africa between 1803 and 1806 (Näf-Gloor 2019). On his return to Germany, Lichtenstein handed his herbarium to Count von Hoffmannsegg (a renowned botanist and entomologist) to be later incorporated into the Willdenow Herbarium (Näf-Gloor 2019). The annotation 'Hoffmannsegg' in the bottom right corner of the specimen indicates that the specimen was received from Hoffmannsegg and 'W' is the mark of the Willdenow Herbarium (Hiepko 1972). Both these annotations are in Schlechtendal's handwriting as well as the name 'Lichtenstein' in brackets (Figure 1). According to Hiepko (1972: III), 'very often Schlechtendal noted the name of the writer of the labels between parentheses. When they were available, the descriptions by Willdenow were put on the outside of the folder along with the serial numbers. To facilitate the filming of the herbarium, the sheets were placed on the folders so that the handwritten Willdenow descriptions appear at the bottom right' (Hiepko 1972: III, IV) (see Figure 2).

Until recently, *Adhatoda divaricata* Nees has been erroneously accepted as the basionym for *Justicia divaricata*. In De Candolle's Prodromus, Nees (1847) overlooked the



94. J. *divaricata Lichtenstein;* floribus axillaribus sessilibus oppositis foliis lineari-lanceolatis submucronatis, junioribus villosis, caule fruticoso divaricato. *Lichtenstein Spicileg. Fl. capens.* MSS.

α. Ramis horizontalibus, ramulis erectis.

β. Ramis erectis, ramulis patentibus determinate oppositis.

11 *

Fruticulus ramosus; rami angulati articulati; ramuli striati pubescentes. Folia majora, (fere pollicaria) sessilia, opposita, lanceolata, basi attenuata, glabra; juniora subfasciculata linearia villosa. Flores sessiles albi, labio inferiore maculâ violaceâ. Calyx profunde quadripartitus, laciniis linearibus. Bracteae binae lineares longitudine calycis. *Hab. in Grootrivierspoort prope fluvium thaigarieb s. Oranjerivier ad montes.* ♄. *Lichtenst.* An haec sit J. *capensis Thunbergii?* (*Prodr. p.* 104.) ob descriptionem nimis brevem aegre decidendum.

FIGURE 3.—Protologue of *Justicia divaricata* (Roemer & Schultes (1817: 163–164)).

publication of Roemer & Schultes (1817) and described *A. divaricata* with two syntypes: the above-mentioned specimen from Willdenow's herbarium and a specimen collected at Winterhoeksberg by Ecklon & Zeyher, housed in the University of Graz, Institute of Plant Sciences Herbarium (GZU). The latter specimen is the holotype of *Gendarussa incana* Nees var. *villosa* Nees (Nees 1841). Roemer and Schultes had access to Lichtenstein's *Spicilegium Florae Capensis* (never published) as they thanked him for the use of the information in his unpublished manuscript (Roemer & Schultes 1817: xviii) and they used 'Lichtenstein' as author citation in their protologue of *J. divaricata* (Figure 3) and referred to his unpublished manuscript. The correct author citation of *J. divaricata* is, therefore, Licht. ex Roem. & Schult.

Justicia divaricata is widely distributed in southern Africa (Figure 4) at altitudes of 100–1 200 m and extends northwards into Angola, Mozambique, Zimbabwe and Zambia. According to the original description of the species, the Lichtenstein specimen was collected in 'Grootrivierspoort prope fluvium tkaigarieb s. Oranjerivier ad montes' (Roemer & Schultes 1817: 164), which is in the vicinity of the current Prieskapoort, ca. 12 km southwest of Prieska in the Northern Cape, South Africa. The oldest specimen of *J. divaricata* in a SANBI herbarium was collected by H.W.R Marloth in 1886 at Kuil (in the Barkly West District, Northern Cape). *Justicia divaricata* is mainly found on plains, hillslopes, in dry watercourses and along edges of pans, with large populations often found under trees and bushes. The species prefers sandy areas, particularly red sand overlying limestone (Munday 1995) (Figure 5a). Munday (1980, 1995) reported that *J. divaricata* acts as a calcrete indicator in southeastern Botswana. *Justicia divaricata* has two flowering periods within a year; a profusion of flowers in autumn and a lesser flush in spring (Munday 1980).

The specific epithet *divaricata* (Latin, meaning 'spreading at a wide angle') refers to the general habit of the species (Figure 5b). The species is not threatened and is categorised as Least Concern (Raimondo et al. 2009) based on the IUCN Red List Category and Criteria (IUCN 2012). It can occasionally become weedy in disturbed areas (Munday 1995; Vollesen 2015).

Description (based on Munday (1995) and Vollesen (2015)).—Much-branched annual, or short-lived perennial shrublet; erect, straggling or semiprostrate, up to 1 m high; stems subglabrous to densely puberulous when young or sericeous, often also with longer pilose hairs and/or stalked capitate glands. *Bark* (if present) cracked, fissured and flaky. *Leaves* subglabrous to variously hairy; petiole not clearly defined; lamina linear to lanceolate or oblanceolate to narrowly obovate, often folded with recurved tips; size very variable, 10–20 (–50) × 1–8(–10) mm; apex subacute to rounded, occasionally emarginate, base attenuate, decurrent to stem; midrib usually

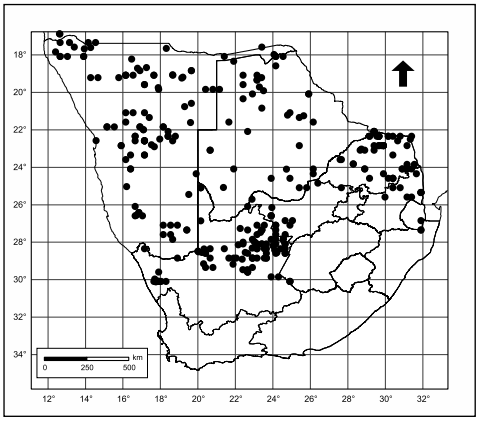


FIGURE 4.—Known distribution of *Justicia divaricata* in southern Africa.

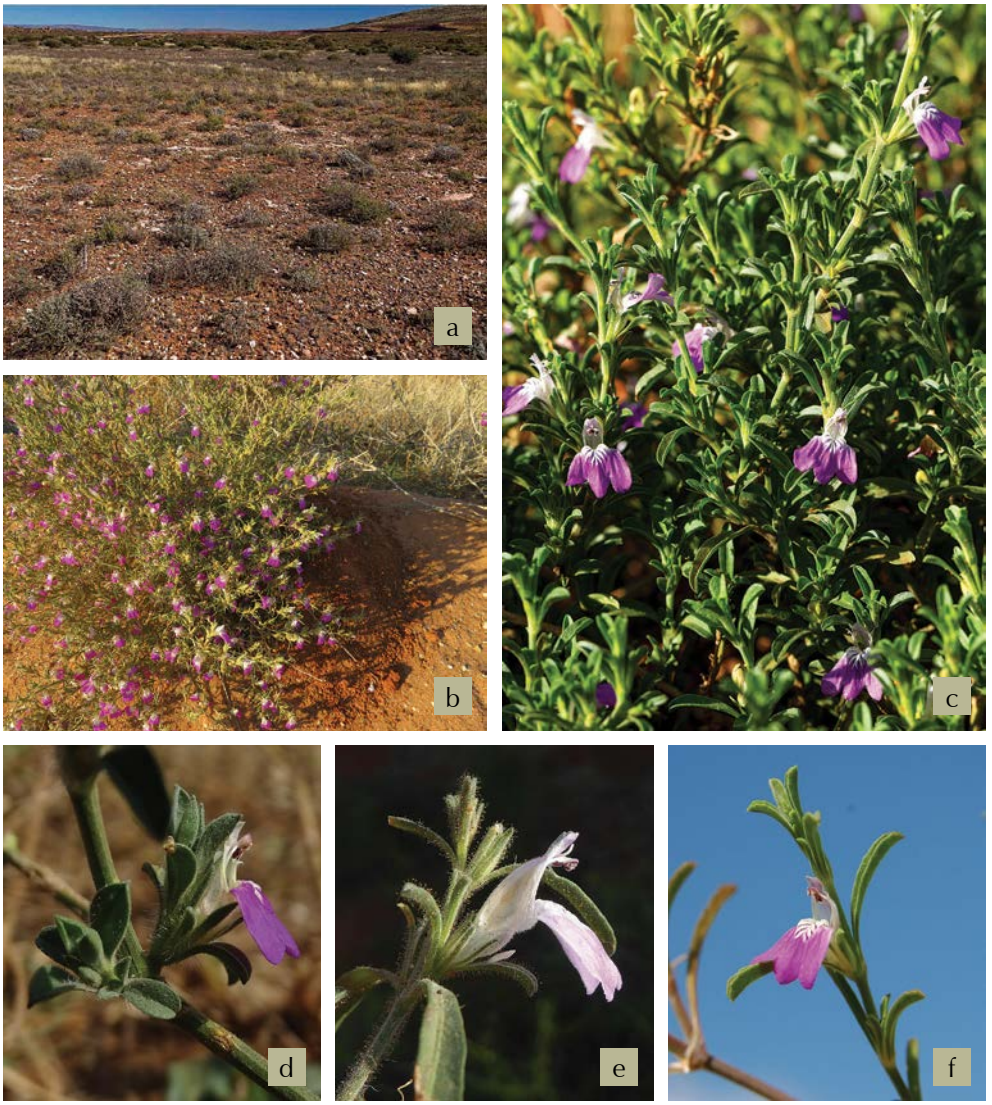


FIGURE 5.—*Justicia divaricata*: a, habitat; b, c, habit; d, e, close-up of flowers showing two-lipped corolla and glandular hairs on bracteoles and calyx; e, f, two-lipped corolla showing rugula. Photographs: a, c, P.C. Zietsman; b, G. Condy; d, M. Koekemoer; e, A. Hankey; f, J. Vahrmeyer.

prominent. *Flowers* subsessile, solitary in axils of foliaceous bracts, sometimes congested towards stem tips; bracteoles linear, green with conspicuous hyaline edges, similar to calyx lobes or slightly longer, oblong to slightly obovate, 5–10(–13) mm long, sparsely to densely puberulous, with or without long pilose hairs and stalked capitate glands. *Calyx* 4-lobed without trace of 5th lobe, green midstripe with conspicuous hyaline edges, 4–6 mm long in flower, lengthening in fruit. *Corolla* often bicoloured, pale mauve to purple (rarely white), with darker lines on lower lip, (7–)10–13 mm long, puberulous; tube 4–7 mm long; upper lip 3–6 mm long, flat; lower lip 5–8 mm long, broadly obovate, lobes rounded. *Filaments*

2–3 mm long; anthers hairy, lower thecae with acute appendage 0.5 mm long. *Capsule* 6–9(–11) mm long, sparsely puberulous or sericeous-puberulous in upper half or near apex only. *Seeds* brown often with intricate patterns (mottled grey and black), glabrous, 2–3 mm in diameter. *Flowering time*: mainly autumn and spring (southern hemisphere). Plate 2378.

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Barleria rigida var. *rigida* Acanthaceae

Namibia, South Africa

Barleria rigida *Nees* var. **rigida** in DC., Prodromus Systematis Naturalis Regni Vegetabilis 11: 242 (1847); Nees: 92 (1850); Anderson: 28 (1863); Clarke: 48 (1901); Obermeyer: 152 (1933); Darbyshire: 49 (2015); Darbyshire et al.: 17 (2019b). *Barleria stimulans* E.Mey. ex Nees var. *macracantha* Nees: 241 (1847). *Barleria irritans* Nees var. *rigida* C.B.Clarke: 48 (1901), pro parte excl. *Schinz 3*.

The family Acanthaceae was estimated to include almost 4 000 species in 242 genera (The Plant List 2013) and more recently over 5 000 species (POWO 2021), occurs mainly in the tropics and subtropics, and displays a wide range of morphology and habitat tolerances. Members may be herbs, lianas, trees or even mangroves (Schwarzbach & McDade 2002). They may be annual, mass-flowering and monocarpic, or perennial. Flowers may be inconspicuous or spectacular. Bracts may be plain green and small, or large and brightly coloured. Flowers vary from radially symmetrical to highly zygomorphic and may be white, green, yellow, red, lilac to magenta and dark purple, and anything in-between. Pollinators include moths, butterflies, bees, long-tongued flies and birds. The family is also renowned for its diversity in pollen morphology (Scotland & Vollesen 2000). In southern Africa, 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 (Balkwill & Welman 2000). The fruit may contain a single seed (very rare), two seeds or two rows of seeds; some members of the family have rough seeds, some smooth and some seeds are covered in hygroscopic hairs (Balkwill & Welman 2000). Some members of the family have a long history of being used as ornamentals, while others appear to be favoured for browsing by some species of antelope (Yazezew et al. 2011). The leaves of members of the type genus are highly architectural and inspired the capitals on columns in Greek Corinthian order and Roman Composite order architecture (Strong 1963).

The genus *Barleria* L. is large with an estimated 335 species globally (Darbyshire et al. 2019b) with at least 60 species occuring in southern Africa. *Barleria* has a mainly palaeotropical distribution with its highest diversity in tropical and southern Africa, and Madagascar (Darbyshire et al. 2019a). Eight centres of endemism have been recognised in Africa including Madagascar (Balkwill & Balkwill 1998; Darbyshire et al. 2019a), with the highest number of endemics now known to occur in Angola, Tanzania and Madagascar (Darbyshire et al. 2019a). It has a wide diversity of morphology, from herbs and creepers to large woody shrubs and even trees (Darbyshire & Luke 2016). Bracts and bracteoles may be leaf-like or spiny. Flowers are usually very noticeable and attractive and may be white, yellow, red or lilac through to purple. One species, *B. ovata* E.Mey. ex Nees, may even have yellow, lilac and dark purple corollas in the same population, which all dry to very dark purple in herbarium specimens. Corollas range from subactinomorphic to very strongly zygomorphic

PLATE 2379.—1, flowering branches, × 0.5; 2, inner calyx lobes, × 2; 3, capsule, × 2; 4, bracteoles, × 2; 5, posticous calyx lobe, × 2; 6, anticous calyx lobe, × 2; 7, bracteoles and calyx, abaxial view, × 2. Voucher specimen: *Condy s.n.* in National Herbarium, Pretoria. Artist: Gillian Condy.

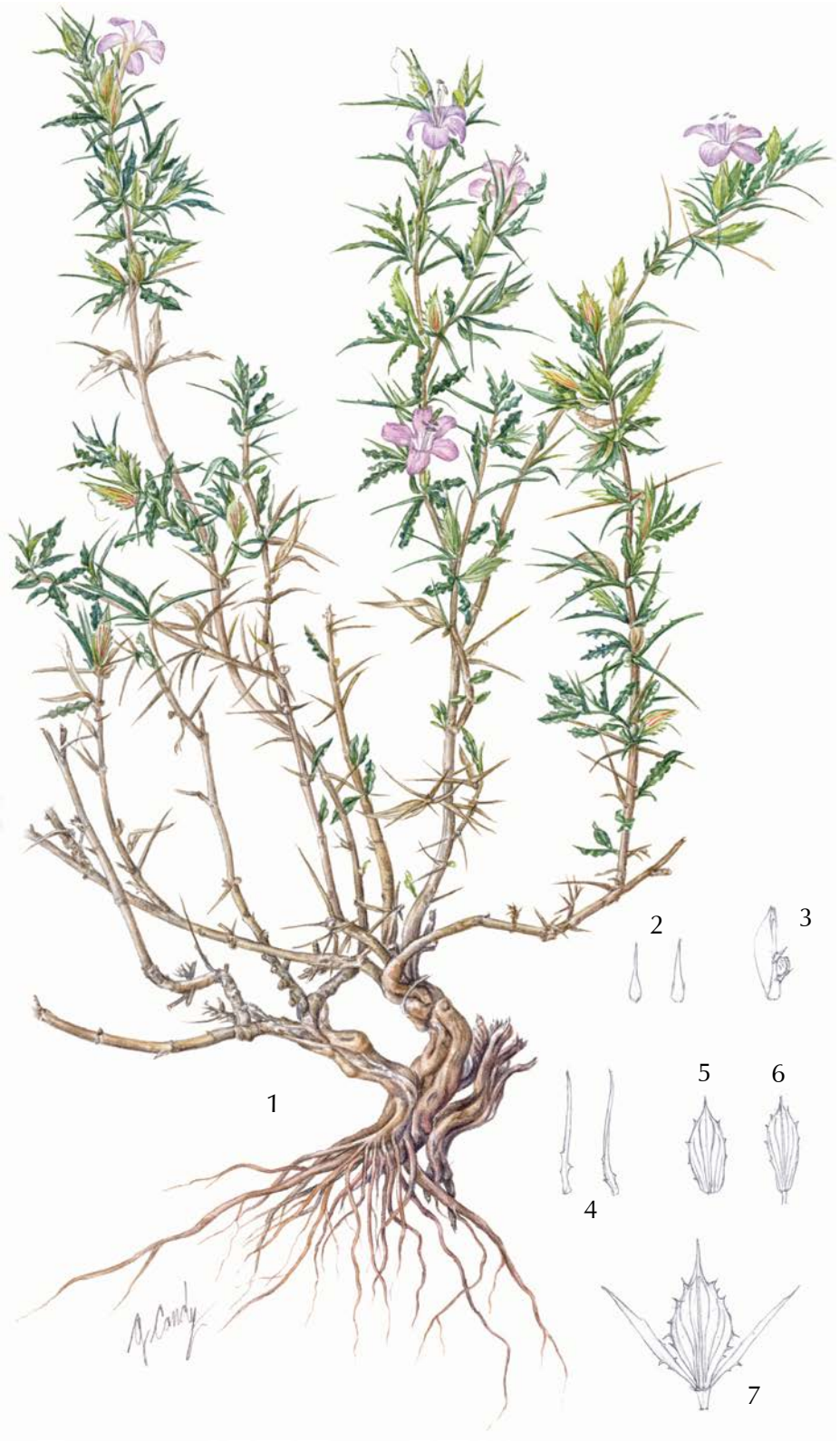

PLATE 2379 *Barleria rigida* var. *rigida*

and the androecium may have from two to four stamens and one staminode, with any combination in-between. Species of *Barleria* occur in a variety of habitats, including on sea-facing dunes, in forests, savanna, grassland or semi-desert. They may have two or four seeds in the beaked or unbeaked capsules and the seeds are covered in hygroscopic hairs, except where they have been secondarily lost in *B. descampsii* Lindau and allies (Darbyshire 2009). The pollen is spherical, deeply reticulate and usually porate (Scotland & Vollesen 2000). *Barleria repens* Nees, *B. obtusa* Nees and what is probably a hybrid between *B. repens* and *B. gueinzii* Sond. are cultivated locally, while *B. cristata* L., the type of the genus, is cultivated internationally.

Barleria has been variously subdivided into subgenera, sections and informal groups and current research by Iain Darbyshire of the Herbarium, Royal Botanic Gardens, Kew, and collaborators are using molecular data to build a complete phylogeny of the genus in order to facilitate understanding of the evolutionary relationships within this very diverse group. The most recent results uphold *Barleria* as monophyletic, support two subgenera and reduce the number of sections from seven to three (Darbyshire et al. 2019a). Further work by Robert Comito and team using RADseq phylogenomics should provide further insight.

In South Africa, *Barleria* was revised for *Flora Capensis* in 1901 (Clarke 1901) and subsequently by Obermeyer (1933). Thereafter, some new taxa have been described and Mandy-Jane Balkwill (= M.-J. Cadman) undertook a study of the subdivision of the genus (Balkwill 1993) and while engaged in that study described some new species, including the spectacular *B. greenii* M.Balkwill & K.Balkwill (Balkwill et al. 1990). Florence C. Nyirenda has undertaken an appraisal of the southern African species of an informal group circumscribed by M.-J. Balkwill (Balkwill 1993) in *Barleria* Section *Barleria* (Nyirenda 2012) and in doing so, has provided an understanding of the significance of morphological variation in the *B. rigida* complex (Nyirenda & Balkwill 2018). Iain Darbyshire et al. (2019b) have appraised the complex for Angola and Namibia and have brought further deep insight to understanding the variation in this difficult group.

Barleria rigida has affinities with *B. irritans* and *B. bechuanensis* C.B.Clarke. The leaf margins of the latter have no teeth, whereas those of *B. rigida* are variously toothed. *Barleria rigida* and *B. irritans* are most readily separated based on geography, with *B. irritans* being present in the Eastern Cape and *B. rigida* in the Northern Cape and northwards (Nyirenda 2012). The calyx lobes of *B. irritans* are longer than 20 mm, whereas those of *B. rigida* are up to 18 mm long. The leaves of *B. rigida* var. *rigida* are usually narrowly elliptic and have slightly undulate to markedly undulate leaf margins that are often white and markedly thickened. They sometimes have few teeth or they may have regularly arranged teeth on the margin, with the teeth rarely longer than 1 mm. The leaves of *B. rigida* var. *ilicina* (E.Mey. ex T.Anderson) Oberm. are broadly elliptic and the margins may be flat or irregularly undulate and are often white and slightly thickened. They are always toothed, although there may sometimes be fewer teeth than in var. *rigida*, and at least some teeth are longer than 1.5 mm and on many specimens the teeth may be 3–4 mm long. There are some undescribed species that are similar to *B. rigida* and there are additional varieties within the species that also need description (Nyirenda 2012).

Barleria rigida was described by Christian Gottfried Daniel Nees von Esenbeck (Nees) in the 1847 Volume 11 of Augustin Pyramus de Candolle's *Prodromus Systematis Naturalis Regni Vegetabilis*. Three specimens are cited in the original description and one has been selected as the lectotype by Darbyshire et al. (2019b). This specimen presents an interesting mystery. Firstly, there is no locality information on the sheet and Nees gave a very vague locality, 'Africa australi extratropical'. Secondly, there is no date of collection on the sheet. Thirdly, the apparent collector, Hoffmannsegg, was a well-known botanist and entomologist, but his name does not appear as a collector or in the index of the two editions of *Botanical Exploration of southern Africa* (Gunn & Codd 1981; Glen & Germishuizen 2010). Knowing that there is an *Acanthopsis hoffmannseggiana* (Nees) C.B.Clarke in South Africa, it was decided to check whether the type of that species provided any clues. It has the same apparent collector and a similarly vague locality (Steyn & Van Wyk 2015), so did not appear to be of much help. However, by looking at the South African distributions of *B. rigida* and *A. hoffmannseggiana*, one finds that the area of overlap is in the Northern Cape, in the broader Orange River valley. If the two species were collected by the same collector, on the same trip, it gives a better idea of where they may have been collected. A search for records of Johannes Centurius von Hoffmannsegg (1766–1849) visiting that area was conducted and a German biography was found (https://saebi.isgv.de/biografie/Johannes_Centurius_von_Hoffmannsegg_(1766-1849)).

Hoffmannsegg was very committed – he sold his inherited estate to his brother-in-law so that he could go on a six-month trip to Portugal. Two years later, he returned to the Iberian Peninsula and stayed for four years. In 1801, he sent Friedrich Wilhelm Sieber to Brazil to collect material to include in his collections. In 1802, his collections were united with those of Johann Christian Ludwig Hellwig. In 1804, he moved to Berlin to coordinate work on his so-called 'Flore Portugaise' and set up a state-of-the-art printing studio to produce it. In 1820, his sister died and he once again inherited the family estate, but it was run down and in debt and he personally was in dire financial straits due to the costs of producing the 'Flore Portugaise'. He then rebuilt the businesses linked to the family estate and then used the proceeds to finish the production of his flora. The biography states that even in his old age, he planned an extended expedition to Africa, but it never came to fruition. There are types from Brazil that bear the name Hoffmannsegg, for example *Salvinia rotundifolia* Willd., but Sieber's name does not appear on the specimen. It seems that Hoffmannsegg's practice must have been to include his name on specimens to indicate that they were in his herbarium, rather than that he had collected them. This, however, does not solve the mystery of how two South African species have types that were apparently collected by Hoffmannsegg.

Another online search revealed that Martin Heinrich Lichtenstein (1780–1857) had sent plant specimens to Willdenow and Hoffmannsegg in Berlin (Gunn & Codd 1981). It seems then that the type of *Barleria rigida* was collected by Lichtenstein. On the accompanying text of the scanned specimen in JSTOR Global Plants, the collector was given as M.H.C. Lichtenstein with the following notes provided: 'The scientific names of the Willdenow Herbarium specimens in B are mainly left without author citation as these names are the historic ones used in the handwritten diagnosis by C.L. v. Willdenow on the species folder. D.FL. v. Schlechtendal, who sorted the Herbarium according to the Linnaean system, brought it to the present state and annotated the mounted specimens with these

names. His enumeration, based on these names, is used in the physical arrangement of the Willdenow Herbarium at B. Schlechtendal's annotations of personal names in the lower right corner of the sheets represent the person from which Willdenow received the material, which is not necessarily the collector. Only some of the specimens are further annotated. Names of collectors, donors, determiners or exchanging herbarium keepers are cited in the annotations field.' This is consistent with our independent conclusion that the specimen must have been collected by Lichtenstein, rather than by Hoffmannsegg. Nees states that the Hoffmannsegg and Lichtenstein specimens were collected in 'Grootriviers Poort', but this locality is outside of the known distribution of the species. The specimen that Nees attributed to Lichtenstein was in the main Berlin collection and was sadly destroyed in World War II, making it impossible to check the locality or for a date on its label.

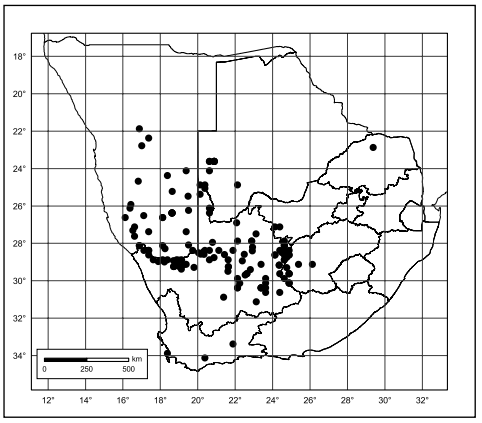

FIGURE 1.—Distribution of *Barleria rigida* var. *rigida* in southern Africa.

William John Burchell's specimen, that is a syntype, has the number 1992 and the Kew sheet bears the following locality: 'Kalahari Region, Hay Division, Griqualand West, Plains between Griqua Town and Witte Water' and McKay (1943) indicates that it was collected on 14 February 1812. Therefore, it took 41 years from the first collection and a further 35 years from the second collection until the species was described.

Barleria rigida var. *rigida* is known from many specimens (over 20) with widespread distribution occurring mainly in the Upper Karoo and part of the Gariep Desert and Kalahari Karroid Shrubland (Mucina & Rutherford 2006). This variety of the species occurs in southern Namibia and in the Northern Cape Province of South Africa (Figure 1). It grows in deep or shallow red-yellow sandy soils, or in gravelly, stony or rocky light grey soils with underlying dolerite or calcrete and components of shales and mudstones. The variety occupies altitudes ranging from 400 to 1 500 m above sea level. Plants near the type locality occur in the transitional fragmented Upper Karoo and Dry Highveld Grassland, in the Besemkaree Koppies Shrubland near where the Northern Cape and North West provinces border with the Eastern Cape. The Besemkaree Koppies Shrubland consists of dolerite koppies and soils embedded within Karoo Supergroup sediments (Mucina & Rutherford 2006). Based on it occurring widely in the Northern Cape and being locally common in many of the areas where it occurs, Darbyshire et al. (2019b) have recommended a Red List status of Least Concern.

Specimens have been collected in flower between December and June, with a very strong peak in March. There is no record of attempts to cultivate *Barleria rigida*. It has been found, however, that species of Acanthaceae that occur in dry areas do not easily grow from cuttings and it is difficult to find under which conditions they will flower in cultivation.

Dryland species are also vulnerable to fungal attack when cultivated in mesic conditions, due to more water being available than in their natural habitat. Like many members of the Acanthaceae, *B. rigida* is browsed by livestock and indigenous game species.

The specific epithet, *rigida*, means 'rigid' and no doubt refers to the rigid bracteoles with reduced blades that form sharp rigid spines.

Description.—Perennial woody shrublet. *Stems* arising from a woody rootstock and branching above the ground, up to about 300 mm high or more; old stems glabrescent; young stems may be bifariously hairy or covered in very short hairs. *Leaves* narrowly ovate, 7–30 × 1.5–6.0 mm, usually glabrous; leaf margin undulate, entire or with small teeth; petiole short, 0.5–2.0 mm long. *Inflorescence* usually of solitary flowers but sometimes in clusters of 1–5, borne in alternate axils. *Bracteole* rigid, lanceolate, v-shaped in cross section, 11–24 × 1–4 mm, with a faint vein parallel to the thick midvein, hardened; margin with a few small, scattered teeth up to 1 mm long or occasionally entire; base truncate. *Calyx* outer lobes ovate, glabrous, with or without a purplish tinge on veins and pale sections at the base, membranous, papery, cartilaginous or indurate; margins serrate or weakly spine-toothed; posticous lobe 13–23 × 3–9 mm; anticous lobe 10–21 × 3–9 mm; inner calyx lobe margins entire. *Corolla* white, cream, pink, lilac, mauve, blue or purple, glabrous or shortly pubescent with microscopic hairs. *Stamens* long-exserted, inserted near middle of corolla tube; filaments 16–24 mm long; anthers 1.4–2.6 mm long; lateral staminodes 1.0–2.7 mm long, pubescent basally; antherodes 0.3–0.9 mm long. *Ovary* narrowly ovoid, with white hairs at apex; style exserted; stigma slightly swollen. *Fruit* a capsule, oblong fusiform, 8–13 × 3–5 mm. *Seeds* discoid with dense, matted hygroscopic hairs. *Flowering time*: January to June. Plate 2379.

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Tarchonanthus parvicapitulatus Asteraceae: Tarchonantheae

Namibia, South Africa, Zimbabwe

Tarchonanthus parvicapitulatus *P.P.J.Herman*, Bothalia 32: 26 (2002); Boon: 588 (2010); Cron et al.: 669 (2019).

Tarchonanthus L. and *Brachylaena* R.Br. are the only two genera included in the tribe Tarchonantheae of the family Asteraceae (Ortiz 2009). These are two of only a few genera in the family Asteraceae of which the members may develop into proper trees. The tribe Tarchonantheae, together with the tribes Oldenburgieae, Dicomeae and Cardueae, comprise the subfamily Carduoideae (Ortiz 2009). From the ITS trees presented for this subfamily by Ortiz (2009) and Ortiz et al. (2009), it is clear that the tribes Tarchonantheae and Oldenburgieae (containing only the South African endemic genus *Oldenburgia* Less.) are more closely related and situated far from the other tribes in the subfamily Carduoideae.

Species of *Tarchonanthus* and *Brachylaena* are dioecious, meaning that male and female florets are borne on separate plants (Figures 1–3). The female florets contain, besides the corollas, only fertile pistils (Figure 3b). The male florets contain the fertile stamens and a sterile pistil (Figure 2a, b). The sterile pistil in the male floret is, however, functional in that it serves as a pollen presenter. When the corolla of the male florets is still closed, the pollen is released from the anthers onto the young, included, distal portion of the style, which is usually unbranched or rarely has two small lobes (Figure 2a, b). The corolla lobes then open, the style starts elongating, carrying with it the numerous pollen grains. When outside the confinement of the corolla, the pollen is available to be collected by insects or blown away by the wind.

Representatives of the genus *Tarchonanthus* can be distinguished from representatives of the genus *Brachylaena* by the florets lacking a pappus and the presence of cottony woolly hairs enveloping the cypselae (indehiscent, single-seeded, dry fruit), the latter suggesting wind as an obvious mode of dispersal (Figures 1m, 3d). It has also been suggested that plant species with seed/fruit firmly embedded in cottony coverings are adapted for directed dispersal by birds as nest material (Dean et al. 1990). The woolly fruit of *Tarchonanthus* are reminiscent of those of *Eriocephalus* L. (commonly known as *kapokbosse*, Afrikaans for 'snow bushes'). The fruit of many *Eriocephalus* species are abundantly present in the nests of birds (Dean et al. 1990). We suggest that birds may, in a similar manner, contribute to fruit dispersal in *Tarchonanthus*. The hairs in the capitula of *Tarchonanthus* and *Eriocephalus* species were described by Herman (2001) as being rather similar in having transverse walls (septate hairs). Despite this similarity, *Tarchonanthus* differs from *Eriocephalus* in having the

PLATE 2380.—1, leafy twig, × 1; 2, branchlet with male synflorescences, × 1; 3, male capitulum, × 2; 4, male floret, × 2; 5, branchlet with female synflorescences, × 1; 6, fruiting branchlet, × 1; 7, mature cypsela covered in woolly hairs and tipped by dried remains of the female floret, × 4; 8, cypsela in longitudinal section and with hairs removed, × 4; 9, habit of multi-stemmed tree, ± 4 m tall. Voucher specimens: sterile twig, *Hyde-Johnson 114*; male plant, *Hyde-Johnson 115*; female plant, *Hyde-Johnson 116*, all in H.G.W.J. Schweickerdt Herbarium, Pretoria. Artist: Jenny Hyde-Johnson.

PLATE 2380 *Tarchonanthus parvicapitulatus*

cottony hairs on the cypselae interspersed with numerous glandular hairs (Figure 3c). In addition, the capitula of *Eriocephalus* are bisexual, with fertile outer female florets and central functionally male florets and with paleae on the receptacle. *Eriocephalus* also belongs to a different tribe: the tribe Anthemideae.

Tarchonanthus is confined to sub-Saharan Africa, with its centre of diversity in southern Africa. This is the second species of *Tarchonanthus* to be figured in this series, the first being *T. obovatus* DC. (Herman & Condy 2001). When not in flower, members of the genus may be readily identified by the leaves being distinctly discolorous, white-felted on lower surface, green and minutely puckered with glandular reticulation on upper surface (Figure 4c), and with a strong smell of camphor when crushed. The latter property of the leaves is the

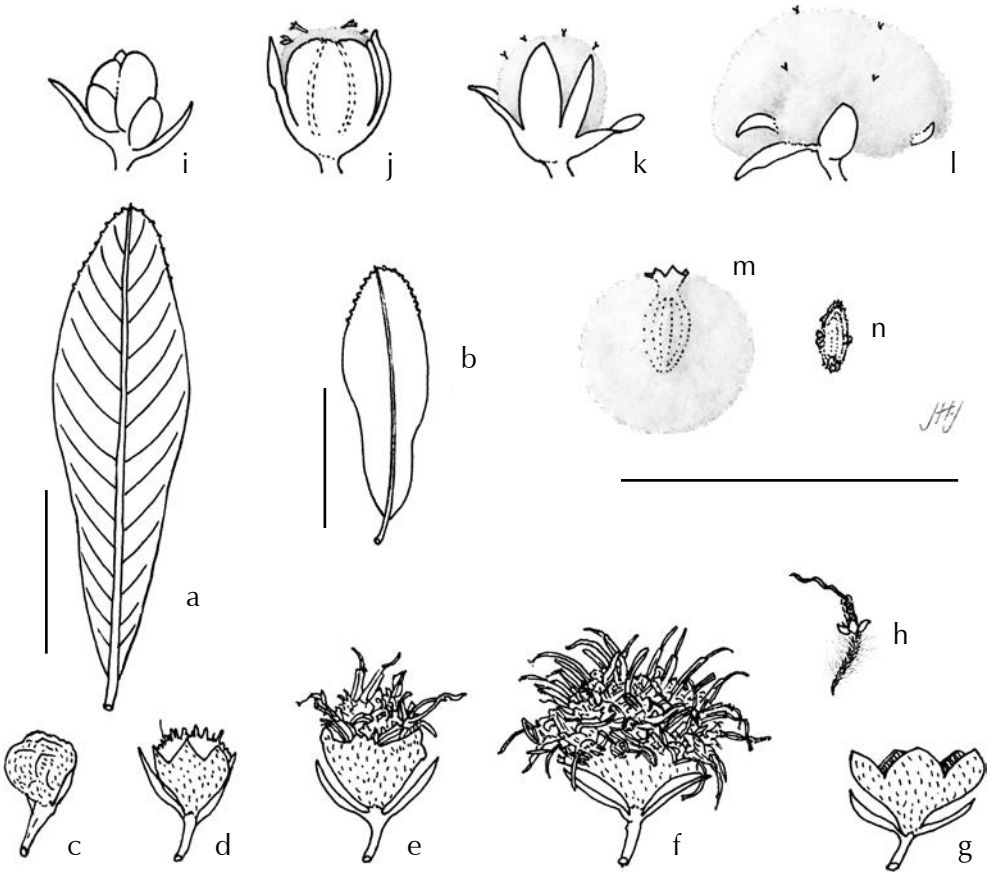

FIGURE 1.—*Tarchonanthus parvicapitulatus*, details of leaf, capitula, floret and fruit morphology: a, leaf towards upper end of size, upper surface; b, leaf towards lower end of size, lower surface; c–h, male capitulum showing developmental sequence of anthesis of florets (c–f), involucral bracts beige-felted on the outside (g) and a fading male floret (h); i–n, female capitulum showing developmental sequence ending in mature fruit (i–l), ribbed mature cypsela covered by wool (m), and as seen in side view with the wool and remains of the corolla removed (n). Vertical scale bars: a, b, 10 mm. Horizontal scale bar: c–n, 10 mm. Artist: Jenny Hyde-Johnson.

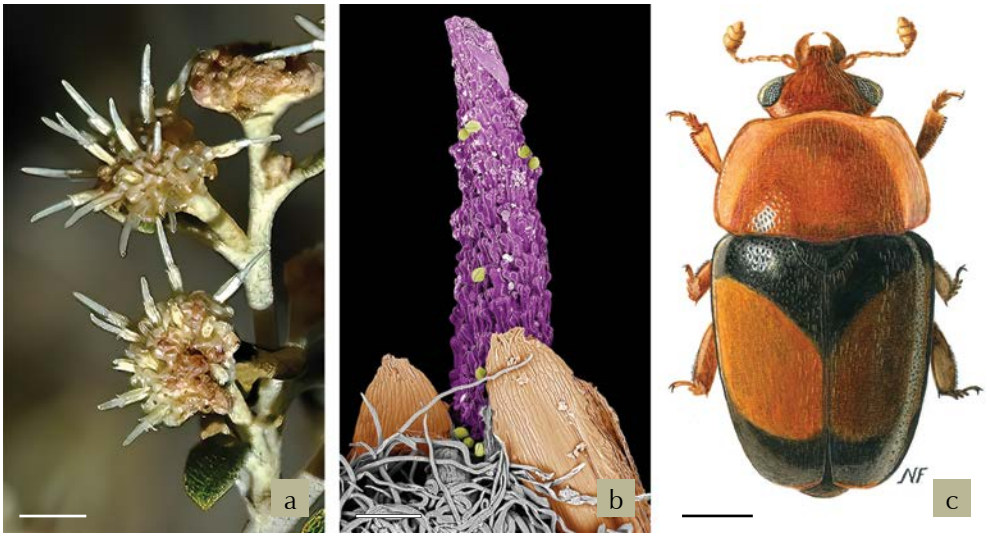

FIGURE 2.—*Tarchonanthus parvicapitulatus*, morphology of male synflorescences and associated pollen beetle (Coleoptera: Nitidulidae: Meligethinae): a, male capitula, distal one with florets still closed, the open florets showing long-exserted styles surrounded by ring of anthers; b. SEM micrograph of male floret with anthers (orange) and elongated style (purple), the latter serving as pollen presenter and still carrying a few pollen grains (yellow) (from *Barker 886* in PRE); c, *Tarchonanthogethes fasciatus*, one of at least four species of pollen beetle that have their larvae associated with the male capitula of *Tarchonanthus parvicapitulatus*. Scale bars: a, 5 mm; b, 100 μm; c, 0.25 mm. Photographs: a, J. Hyde-Johnson; b, P.P.J. Herman. Artist of c: Niccolò Falchi, from Audisio et al. (2015) in *Zootaxa* 3920: 101–152, reproduced by kind permission of Magnolia Press and P. Audisio.

source of the vernacular names camphor bushes or *kanferbosse* (Afrikaans) for members of the group. However, despite the camphor-like smell, plants were found to contain only very small amounts of camphor (0.4%), the major essential oils being α-fenchyl alcohol (29.1%), 1,8-cineole (16.5%) and α-terpineol (8.5%) (based on hydrodistillation of leaves of *T. camphoratus* s.str. from near Naivasha, Kenya) (Mwangi et al. 1994).

Following the taxonomic revision of *Tarchonanthus* by Paiva (1972), only two species of *Tarchonanthus* were recognised by most workers in Africa, the polymorphic *T. camphoratus* L. and *T. trilobus* DC., the latter with two varieties. However, based on a taxonomic reassessment of the *Tarchonanthus camphoratus* specimens housed in PRE, the complex was split into five separate species (Herman 2002). Two previously described species were reinstated, namely *T. minor* Less. and *T. obovatus*. Both had been placed in synonymy under a broadly defined *T. camphoratus* by Paiva (1972), an approach also followed by, amongst others, Hilliard (1977), Pope (1992) and Beentje (1999). In addition, two new species, namely *T. littoralis* P.P.J.Herman and *T. parvicapitulatus*, were described, leaving *T. camphoratus* in the narrower sense. Four of the five species are confined to southern Africa (the part of the African continent south of the Kunene, Okavango and Zambezi rivers), whereas *T. camphoratus* is widespread, ranging from southern Africa through East Africa to the Horn of Africa.

Apart from *Tarchonanthus trilobus*, the five species recognised by Herman (2002) in the *T. camphoratus*-complex were separated on the grounds of leaf and inflorescence

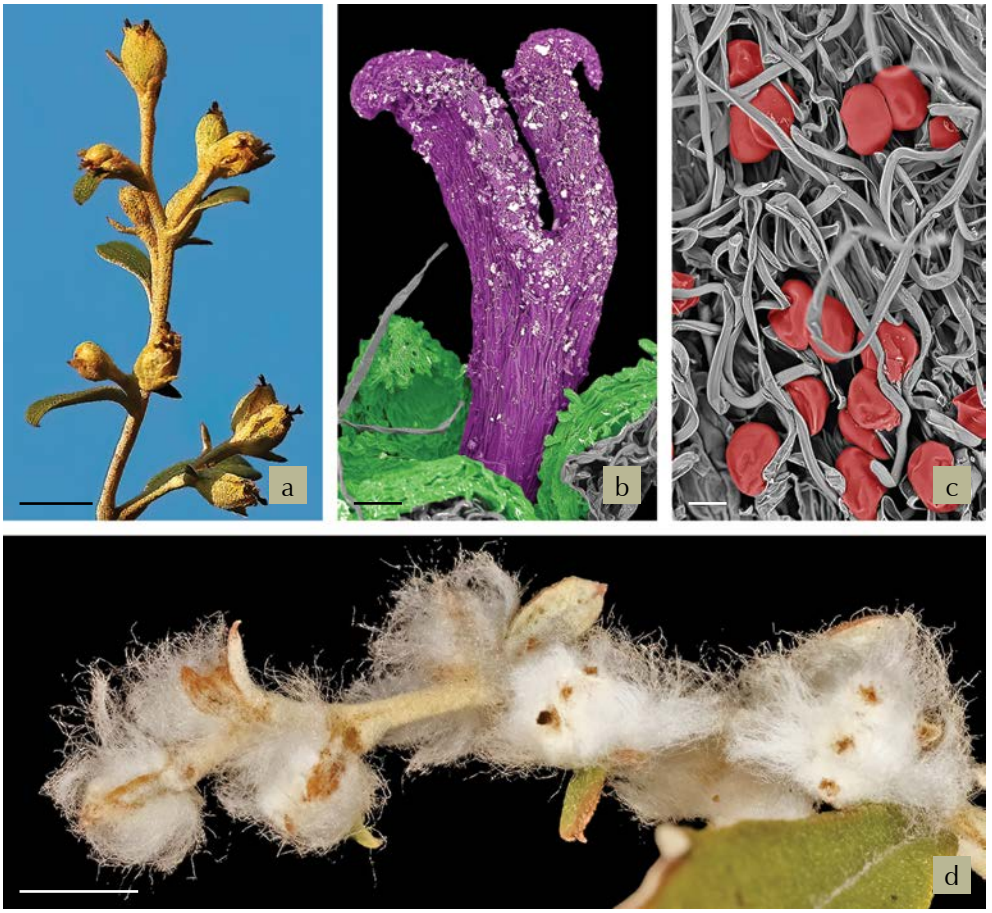

FIGURE 3.—*Tarchonanthus parvicapitulatus*, morphology of female synflorescences and fruit: a, female capitula, relatively young with exserted black styles; b. SEM micrograph of female floret with petals (green) and short style ending in two style branches (purple) (from *Ward 1402* in PRE); c, SEM micrograph of mature cypsela surface to show globular glandular hairs (red) amongst the dense cover of woolly hairs (from *Ward 2612* in PRE); d. mature fruiting capitula filled with cypselae covered by white cottony hairs. Scale bars: a, 4 mm; b, 50 μm; c, 25 μm; d, 4 mm. Photographs: a, J. Hyde-Johnson; b, c, P.P.J. Herman; d, A.E. van Wyk.

characters, flowering time, distribution and habitat in South Africa. In *T. minor* both the male and female synflorescences are densely spicate, the involucral bracts of both the male and female capitula (flower heads) are free and its peak flowering time extends from September to December (spring to early summer in the southern hemisphere). In *T. parvicapitulatus*, *T. camphoratus*, *T. obovatus* and *T. littoralis*, the male and female synflorescences are laxly paniculate, the involucral bracts of the male capitula are fused halfway (Figure 1d–g) while those of the female capitula are free (Figure 1k, l), and the peak flowering season of these four taxa extends from February to August (late summer, autumn and winter in the southern hemisphere). In *T. parvicapitulatus* and *T. littoralis* the leaf margins are usually faintly denticulate, at least towards the apex of the leaves (Figures 1a, b, 4c), whereas the leaf margins of *T. camphoratus* and *T. obovatus* are always entire. *Tarchonanthus*

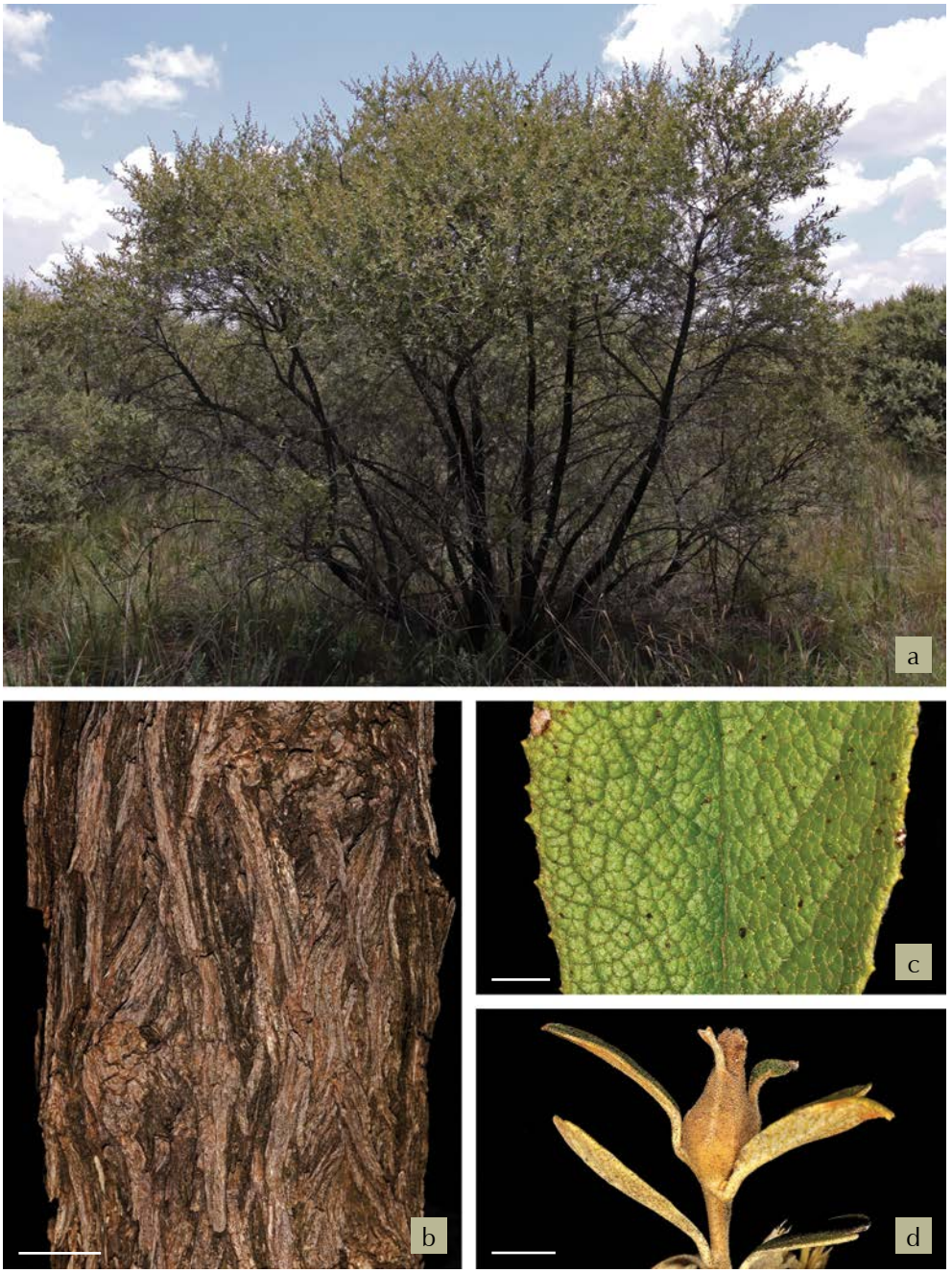

FIGURE 4.—*Tarchonanthus parvicapitulatus*, habit and vegetative morphology: a, multi-stemmed shrub, ± 4 m tall, growing as part of a dense population of the species in grassland on dolomite at Kalkheuvel West, Broederstroom, Gauteng; b, bark; c, middle portion of leaf blade viewed from above and showing puckered surface, glandular reticulations and faintly denticulate margin (though often entire); d, characteristic stem-tip gall, most probably caused by an insect. Scale bars: b, 20 mm; c, 2 mm; d, 5 mm. Photographs: A.E. van Wyk.

parvicapitulatus is distinguished from *T. littoralis* by the small capitula (fruiting capitula up to 10 mm in diameter), the smaller leaves with shorter petioles and its inland distribution. *Tarchonanthus littoralis* has large capitula (fruiting capitula up to 15 mm in diameter), large leaves on fairly long petioles and occurs along the coast from southern KwaZulu-Natal to the Western Cape. *Tarchonanthus camphoratus* differs from *T. obovatus* by the usually creamy or yellowish cottony hairs enveloping the cypselae (fruits), the narrowly elliptic to slightly narrowly oblanceolate leaves with a grey-green or khaki-green colour. In *T. obovatus* the cottony hairs enveloping the cypselae are usually pure white, the leaves are obovate to elliptic and usually distinctly discolorous with a bright green upper surface and a densely white pubescent lower surface. It also has a narrow geographical range, being confined to the Griqualand West Centre of Endemism (Van Wyk & Smith 2001; Frisby et al. 2019), whereas *T. camphoratus* s.l. has a much wider distribution. In a recent publication, Aro et al. (2021) described the usage of additional characters to distinguish between *T. camphoratus* and *T. parvicapitulatus* as well as the medicinal properties of the two taxa.

Based on the flowering times of *Tarchonanthus parvicapitulatus*, *T. camphoratus*, *T. obovatus* and *T. littoralis* reported by Herman (2002) and those of *Brachylaena* species supplied in correspondence by one of us (PPJH), the Italian entomologist P. Audisio and co-workers were able to identify, for the first time, the previously unknown larval host-plants of African members of the pollen beetles in the *Anthystrix*-complex of beetle genera, namely species of *Tarchonanthus* and *Brachylaena* (Audisio et al. 2008). They subsequently described the new genus *Tarchonanthogethes* (Audisio et al. 2009, 2015) for the pollen beetles associated with the male capitula of *Tarchonanthus* and *Brachylaena* species. At least four species of pollen beetles (Coleoptera: Nitidulidae: Meligethinae) of which the larvae are associated with the male capitula of *T. parvicapitulatus* were described, namely *Anthystrix endroedyi*, *Tarchonanthogethes hystrix*, *Tarchonanthogethes fasciatus* (Figure 2c) and *Xenostrongylogethes cychramoides* (Audisio et al. 2015). As far as other insect-associates are concerned, we have recorded a characteristic swollen stem-tip gall (Figure 4d), presumably by the larva of a moth, on plants in Gauteng. A noteworthy feature of trees of our species in the vicinity of the Magaliesberg is the presence in late summer to winter of clusters of curved and fragile white 'tubes' (5–8 × 2–3 mm), resembling snail shells, glued to leaves and twigs. These are the nymphal tubes of the spittlebug *Tremapterus* sp. (Hemiptera: Cercopoidea: Clastopteridae sensu Cryan & Svenson 2010). The tubes are constructed from dried spittle masses (Hamilton 2015; S. Neser pers. comm.; R. Stals pers. comm.).

Tarchonanthus parvicapitulatus is characterised by the very small male and female capitula (hence the specific name, from the Latin *parvus* meaning small, and *capitulum* meaning head), and the narrowly to very narrowly obovate leaves with the margins faintly denticulate towards at least the apex of the leaves (Figures 1a, b, 4c). Vernacular names recorded for the species include small-headed camphorbush, camphorbush; *kleinhofiekanferbos*, *kanferbos* (Afrikaans); *monokanekane*, *sefahla*, *sefahlane* (Northern Sotho); *igqeba elimhlope*, *igqebe-elimhlophe* and *isiduli sehlathi* (Zulu) (Van Wyk et al. 2011). *Tarchonanthus parvicapitulatus* is widespread, not in danger of extinction and is listed as Least Concern in the Red List of South African Plants (Von Staden 2018). It occurs in Limpopo, North West, Gauteng, Mpumalanga, KwaZulu-Natal and Eastern Cape provinces of South Africa, as well as in Eswatini (formerly Swaziland), Namibia and Zimbabwe (Figure 5). Plants are associated with grassland, bushveld and thicket, rarely forest; in valleys, on mountain slopes, hills and river

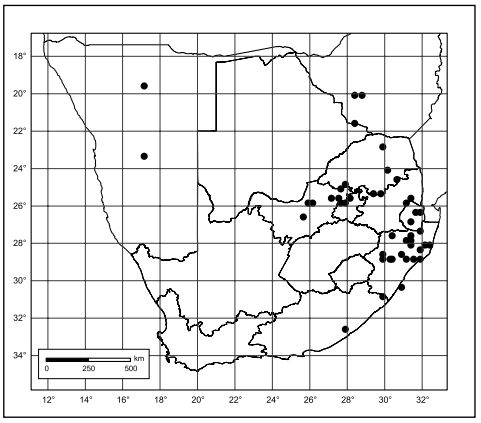

FIGURE 5.—Known distribution of *Tarchonanthus parvicapitulatus*.

banks. In areas where the range of *T. parvicapitulatus* overlaps with that of *T. camphoratus*, it tends to prefer rocky places with relatively shallow soils, whereas the latter seems to favour deeper sandy soils. The rocky habitat provides some protection (especially to the plant's volatile contents) against fire, although the plants are clearly fire-adapted with their thick, tough bark (Figure 4b) on older trunks and stems – often scorched black, a sign of their having survived many veld fires. *Tarchonanthus camphoratus*, on the other hand, is clearly a resprouter and fire-damaged plants rapidly recover. Plants of *T. camphoratus*, in particular, are browsed by game and stock, especially in times of drought (Van Wyk & Van Wyk 2013). *Tarchonanthus parvicapitulatus* is suspected to be utilised in a similar way, with *Ward 7719* (PRE) mentioning that antelope browse coppice shoots of this species. The milk of cows that browsed on leaves of *Tarchonanthus* species is tainted, presumably by the presence of the essential oils (T.W. Naudé pers. comm.).

Members of *Tarchonanthus* are widely used in traditional medicine as well as for many other biocultural purposes (for a review see Nanyonga 2012). Most published information on the uses, chemistry and medicinal properties of the group are based on *T. camphoratus* in a broad sense. No doubt most of these would also apply to *T. parvicapitulatus* and the other segregate species recognised by Herman (2002). Note that although the chemical and pharmacological research by Nanyonga and co-workers referred to in the present contribution are said to be on *T. camphoratus*, it is based on the entity here treated as *T. parvicapitulatus* (plant material collected in the vicinity of Sangoyana in northern KwaZulu-Natal). Volatile extracts of *T. parvicapitulatus* leaves contain a rich assemblage of essential oils with demonstrated antimicrobial and insecticidal properties (Nanyonga et al. 2012, 2013a, 2015). Leaf and bark extracts of this species also showed antioxidant activity, but no significant cytotoxicity (Nanyonga et al. 2013b, c). The oldest validated use of *T. parvicapitulatus* by humans dates from the Middle Stone Age, ~58 000 years ago (Lennox & Bamford 2017; Lennox et al. 2017). The presence of charcoal of *T. parvicapitulatus* associated with heaths was confirmed in the Sibudu rockshelter, an archaeological site with a long history of human occupation in north-central KwaZulu-Natal. These authors suggested that the heavy, hard and aromatic wood (most probably also the leaves) of this species were probably deliberately burned by the early occupants of the cave for its insect-repellent smoke.

The plants illustrated here in the plate and line drawings came from Kalkheuvel West near Broederstroom, northwest of Pretoria, Gauteng, South Africa, and were growing in shallow soil on chert-impregnated dolomite in the transition zone between Highveld grassland and bushveld. In this area, the species prefers fire-protected gullies and the southern aspect of hills. Plants tend to grow gregariously (Figure 4a), a pattern also seen elsewhere

in the distribution range of *Tarchonanthus parvicapitulatus*, as well as for some of the other species – notably *T. camphoratus* in the narrow sense. At Kalkheuvel West it had been noted that antelope such as eland, kudu, gemsbok, hartebeest and duiker prefer to overnight in one particularly dense stand (thicket) of *T. parvicapitulatus* in winter. This is most probably due to shelter provided by the dense stand of leafy shrubs and small trees.

Although little is known about the pollination biology of species of *Tarchonanthus*, the presence of dioecy in all the species, accompanied by mass flowering of the plants, small and inconspicuous florets, the elongated pollen-presenting styles in male florets (Figures 1e, f, h, 2a, b), no detectable floral scent, and the apparent lack of reward in female florets, suggest wind-pollination as one potential mechanism of pollen transfer. This possibility is supported by gregariousness, a trait suggested as being part of the syndrome for wind pollination (Daru et al. 2016). However, counting against wind-pollination is the slightly sticky pollen grains, although this would be a consequence of the need for the pollen to adhere to the stigmatic areas on the style branches. The pollen-carrying styles are well exserted from the male capitula and fully exposed to the wind. Pollen grains are only sparsely present on mature pollen presenters and is presumed to have been dislodged by the wind. In female florets the style with the style branches containing the stigmatic areas, the latter often tinged pink or purple in the fresh state, is also well exserted, but no obvious pollen entrapment mechanisms such as hairy or feathery adaptations are evident. On the other hand, considering that each female floret produces only a single seed, at least theoretically only one viable pollen grain ought to reach the stigmatic areas to ensure fertilisation.

In gardening circles, *Tarchonanthus parvicapitulatus* is still an essentially unknown species. With its relatively small size and dense, evergreen and aromatic foliage, this is certainly a shrub or tree that offers considerable potential as a garden ornamental, bearing in mind that the species is dioecious with the decorative cottony fruiting heads only borne by female plants. Gardens are getting smaller and this necessitates smaller trees that are more suitable than traditional choices. Multi-stemmed plants of this species would also be suitable for planting as a hedge or windbreak (Carr 1994). In nature the most southern populations of the species in Gauteng (Klipriviersberg) can tolerate subzero temperatures, equivalent to at least USDA cold-hardiness Zone 9 (–1 to –7°C; Glen & Van Wyk 2016). Plants in Gauteng are also drought-tolerant and capable of surviving a dry season without significant rainfall of up to about eight months, a period during which they also flower and fruit. Plants from this area should be looked at as a potential resource for selecting horticultural introductions with a combination of cold-hardiness and drought tolerance. No published information on the propagation of this specific species exists. However, Carr (1994) reported that the seeds (with woolly hairs still attached) of *T. camphoratus* in the broad sense sown by him started germinating after 30 to 35 days. Once transplanted into bags, plants were kept under a protective fibreglass cover for the first winter, but thereafter they were quite frost-hardy and progressed rapidly. According to Carr, he made extensive use of the species (most probably the narrowly defined *T. camphorathus*) on his property just north of Johannesburg. Nichols (2005) recommended that when taking cuttings from woody Asteraceae such as *Tarchonanthus*, hard wood from the previous season's growth should be used. In the case of the related *T. littoralis*, cuttings taken in early summer, treated with a rooting hormone and placed in a mistbed with bottom heat, rooted with about 50% success rate (Notten 2008).

Description (mainly after Herman 2002).—Evergreen to semi-deciduous, dioecious shrub or small, multi-stemmed tree, up to 5 m high. *Bark* thick, hard and fibrous, deeply and irregularly longitudinally cracked into anastomosing grooves and ridges. *Leaves* aromatic, alternate, shortly petiolate; petiole 1.5–5.0 mm long; blade narrowly to very narrowly obovate, (22–)25–60(–70) × 7–20(–25) mm; apex obtuse to obtuse-mucronate, sometimes acute; base cuneate; margin often faintly denticulate, at least in distal part, rarely entire; discolorous, upper surface medium to dark green, minutely puckered, hairy when young, becoming glabrous, glandular in reticulations on upper surface, midrib sunken and hairy on the upper surface in lower part of leaf; lower surface densely whitish hairy, main and secondary veins prominent. *Synflorescences* terminal, paniculate. *Male plants*: capitula homogamous discoid, functionally male, 5–9 mm diam., 10–30-flowered; peduncle 0–7 mm long. *Involucral bracts* in single row, fused halfway, 5-lobed, beige-felted abaxially; tube 1–2 mm long, lobes 1.0–1.5 mm long. *Corolla* funnel-shaped, white, fading through pale cream to brownish, glandular and hairy, tube 1.5–2.0 mm long, lobes 5, 1.0–1.5 mm long, apex papillate. *Anthers* 5, exserted, 1.0–1.5 mm long, calcarate, caudate, tails 0.5 mm long, branched; filaments 2–3 mm long. *Style* well exserted, 4.0–5.5 mm long, unbranched or with 2 small lobes. *Ovary* sterile, rod-shaped, 0.5 mm long, covered with septate hairs. *Pappus* absent. *Female plants*: capitula homogamous discoid, functionally female, 3–4 mm diam., 1–3-flowered; peduncle mostly absent or up to 5 mm long. *Involucral bracts* free, in 2 or 3 rows, 2–5 mm long, ± beige-felted abaxially, very narrowly obovate, narrowly ovate or elliptic, acute. *Corolla* funnel-shaped, white, fading through pale cream to brownish, glandular and hairy; tube 0.5–1.0 mm long, lobes (4)5, 0.5–1.0 mm long, papillate. *Style* exserted, 1–2 mm long, bifurcate; style branches 0.5 mm long, often tinged pink or purple in the fresh state. *Ovary* obovate to elliptic, 1.5–3.5 mm long, glandular and septate hairy. *Cypselae* pale or dark brown, obovate, ribbed, 1.5–3.0 mm long, glandular and with pure white cottony, septate hairs. *Pappus* absent. *Flowering time*: March to October with a peak from April to June (autumn to winter in southern hemisphere). Plate 2380.

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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 some other journal or magazine are generally not acceptable for *FPA*.

Authors and/or artists are advised to contact the editor (Alicia Grobler) 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 text 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** by June 2020 to the editor 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* text:

1. ***Synopsis***. The correct name of the plant together with its author/s and relevant literature (name of publication written out in full) 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.' 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 square 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 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. ***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 (full name, not acronym) where the specimen is housed. The caption ends with the name of the artist. Also supply captions for the distribution map and any other figures you want to include (please use scale bars where relevant), making sure all figures are mentioned in the text.

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 done by the resident artist 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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