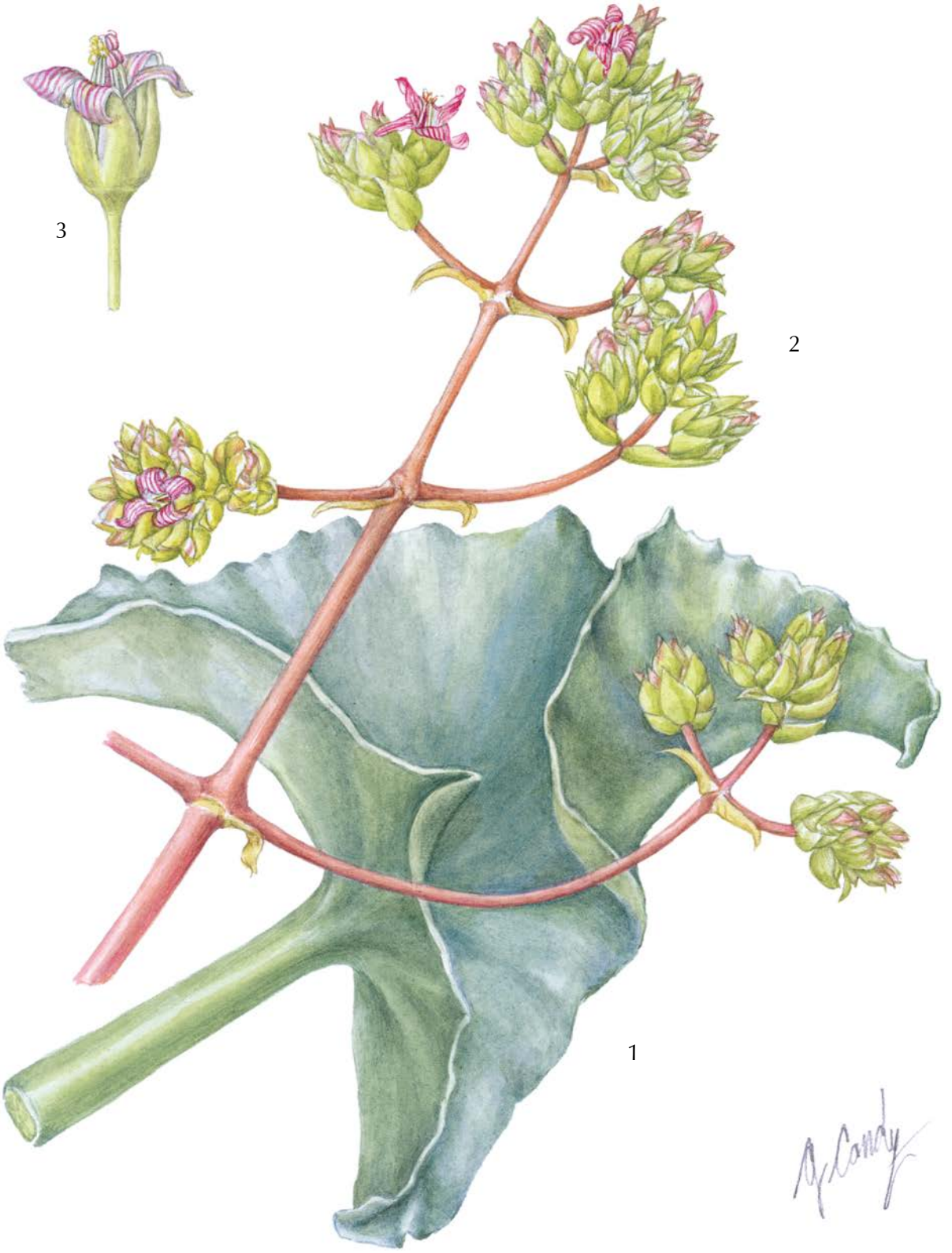

PLATE 2365 *Kalanchoe beharensis*

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).

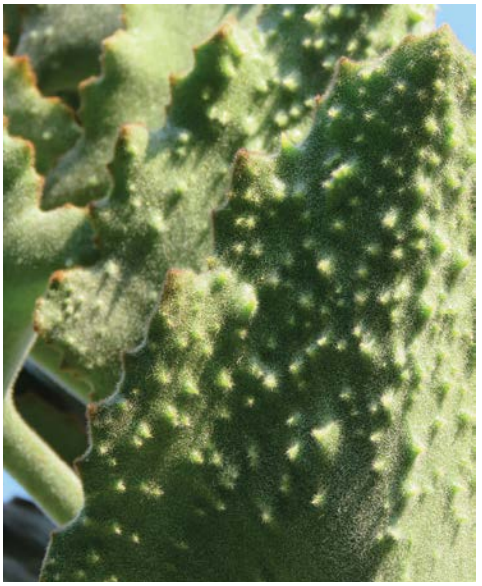

FIGURE 3.—Both the ab- and adaxial surfaces of the leaves of *Kalanchoe* ×*edwardii* 'Fang' are adorned with prominent protuberances. Photograph: G.F. Smith.

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.

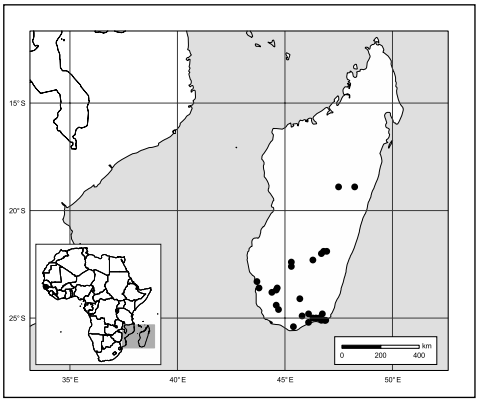

FIGURE 10.—Geographical distribution range of *Kalanchoe beharensis* in Madagascar based on information held in the Global Biodiversity Information Facility, specimens cited in Boiteau & Allorge-Boiteau (1995: 158) that was used for Map 17 [p. 202, page not numbered] reproduced in that work, and other 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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G.F. SMITH[1,*], E. FIGUEIREDO[1], C.C. WALKER[2] and GILLIAN CONDY[3]

[1]Department of Botany, Nelson Mandela University, P.O. Box 77000, Gqeberha [Port Elizabeth], 6031 South Africa.

[2]School of Environment, Earth & Ecosystem Sciences, The Open University, Milton Keynes, MK7 6AA England.

[3]South African National Biodiversity Institute, Private Bag X101, Pretoria, 0001 South Africa.

*Author for correspondence: smithgideon1@gmail.com.