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Two new species of Kalanchoe (Crassulaceae) from western Madagascar

David-Paul Klein, Ralph Mangelsdorff, Rokiman Letsara, Ronen Shtein & Seraina E. Rodewald

Abstract

KLEIN, D.-P., R. MANGELSDORFF, R. LETSARA, R. SHTEIN & S.E. RODEWALD (2025). Two new species of Kalanchoe (Crassulaceae) from western Madagascar. *Candollea* 80: 21–31. In English, English and French abstracts. DOI: http://dx.doi.org/10.15553/c2025v801a3

Two new species of *Kalanchoe* Adans. (*Crassulaceae*) from the Tsingy de Bemaraha National Park, western Madagascar, are described and illustrated, supplemented by detailed notes on their habitat, ecology, and taxonomic position. *Kalanchoe luteola* D.-P. Klein, Letsara & Mangelsdorff is distinguished from other known representatives of *Kalanchoe* subg. *Kalanchoe* from Madagascar by its particularly long, creamy yellow corolla tube. The length of the corolla tube makes *K. luteola* the species with the longest known corolla tube of all Malagasy taxa in the genus. *Kalanchoe manambolensis* D.-P. Klein, Letsara & Shtein is distinguished from *K. aromatica* H. Perrier and *K. bouvetii* Raym.-Hamet & H. Perrier by its indumentum, its corolla length and proportions, and its leaf shape. Both new species' risk of extinction are preliminarily assessed as "Vulnerable" [VU] using the IUCN Red List Categories and Criteria.

Résumé

KLEIN, D.-P., R. MANGELSDORFF, R. LETSARA, R. SHTEIN & S.E. RODEWALD (2025). Deux nouvelles espèces de Kalanchoe (Crassulaceae) de l'ouest de Madagascar. *Candollea* 80: 21–31. En anglais, résumés anglais et français. DOI: http://dx.doi.org/10.15553/c2025v801a3

Deux nouvelles espèces de Kalanchoe Adans. (Crassulaceae) du Parc National de Tsingy de Bemaraha, à l'ouest de Madagascar, sont décrites et illustrées, complétées par des notes détaillées sur leur habitat, leur écologie et leur position taxonomique. Kalanchoe luteola D.-P. Klein, Letsara & Mangelsdorff se distingue des autres représentants de Kalanchoe subg. Kalanchoe connus de Madagascar par son tube de corolle particulièrement long et jaune crème. La longueur du tube de la corolle fait de K. luteola l'espèce avec le plus long tube de corolle connu de tous les taxons malgaches du genre. Kalanchoe manambolensis D.-P. Klein, Letsara & Shtein se distingue de K. aromatica H. Perrier et K. bouvetii Raym.-Hamet & H. Perrier par son indumentum, la longueur et les proportions de sa corolle, et la forme de ses feuilles. Le risque d'extinction des deux nouvelles espèces est provisoirement évalué comme «Vulnérable » [VU] suivant les catégories et critères de la Liste rouge de l'UICN.

Keywords

CRASSULACEAE - Kalanchoe - Madagascar - Melaky - New species - Tsingy de Bemaraha

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Introduction

The genus Kalanchoe Adans. (Crassulaceae) comprises more than 180 species native to Madagascar, Africa, the Arabian Peninsula, Southeast Asia, and northwest Australia. Several recently published molecular phylogeny studies indicate that the genus originated in Madagascar (e.g. RODEWALD et al., 2025), where more than 80 species are endemic. With a total of 20 new taxa of Kalanchoe having been published in the last two decades, the Great Island continues to harbour undescribed taxa, underlining the fact that Madagascar is one of the centres of diversity of the genus. Out of the five subgenera recognised by SMITH (2024) in the genus Kalanchoe, i.e., subgenus Kalanchoe, subg. Bryophyllum (Salisb.) Koord., subg. Kitchingia (Baker) Gideon F.Sm. & Figueiredo, subg. Alatae (Gideon F.Sm.) Raymond-Hamet ex Gideon F.Sm., and subg. Calophygia Desc. emend. Gideon F.Sm., the autonymic subg. Kalanchoe is the only one that is not endemic to Madagascar.

In September 2023, an expedition to the Tsingy de Bemaraha National Park was conducted collaboratively by the Ludwig-Maximilians-Universität in Munich, Germany, and the National Herbarium of the Parc Tsimbazaza (TAN) in Antananarivo, Madagascar. The Tsingy de Bemaraha National Park is a karst landscape situated in the seasonally dry west of Madagascar, located in the district of Antsalova in the Melaky region (Fig. 1). Despite its long collection history of botanical exploration dating back to 1911 with Henri Perrier de la Bâthie (1873-1958), this large site remains botanically poorly explored (Goodman et al., 2018). Only four species of Kalanchoe from this area had been documented prior to the expedition, i.e., K. bogneri Rauh (five known collections) and K. humifica Desc. (one known collection), as well as the two upright-flowered K. boisii Raym.-Hamet & H. Perrier and *K. antennifera* Desc. (both known only by a single collection). Results of the expedition were the rediscovery of *K. boisii*, previously known only from the type material, a new locality for K. berevoensis Rebmann, previously known only from Berevo, c. 65 km south of Bekopaka, and the discovery of three potentially new species of Kalanchoe. Two of these discoveries are described and illustrated here: K. luteola D.-P. Klein, Letsara & Mangelsdorff and K. manambolensis D.-P. Klein, Letsara & Shtein.

Taxonomy

Kalanchoe luteola D.-P. Klein, Letsara & Mangelsdorff, **sp. nov.** (Fig. 2).

Holotypus: Madagascar. Reg. Melaky [Prov. Mahajanga]: Bekopaka, Tsingy de Bemaraha, [19°01'S 44°46'E], 154 m, 22.IX.2023, Rodewald, Shtein, Letsara & Tsiverilaza SER 23-006 (TAN!; iso-: G!, M [M-0356649]!, MO!).

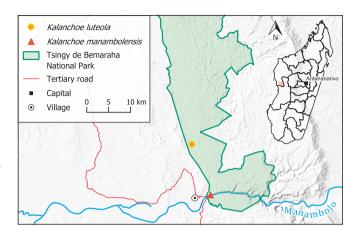


Fig. 1. – Distribution map of the two new Kalanchoe Adans. described from the Parc National de Tsingy de Bemaraha. [map resources: https://earthdata.nasa.gov, Humanitarian Data Exchange (UN OCHA), OpenStreetMap contributors. Map made with QGIS]

Kalanchoe luteola D.-P. Klein, Letsara & Mangelsdorff is distinguished from other Malagasy Kalanchoe species by its particularly long, tubular and salverform, creamy yellow corolla, and by having anthers with an orange globule. Among representatives of Kalanchoe subg. Kalanchoe from western Madagascar, it further differs by being perennial, glabrous except for the flowering shoot and inflorescence, and by having strictly simple leaves.

Plants perennial, medium-sized succulent herbs, to c. 80 cm high, with creeping, apically leafed main axes, basally developing multiple offshoots and forming clusters of numerous sprouts; flowering shoots up to 78 cm high, glabrous except for the distal half, pedicels, and the abaxial side of sepals, corolla tube and petal lobes. Stems terete, to 5.5 mm in diam., up to 70 cm long with up to 9 pairs of leaves on flowering shoots (less when sterile) and internodes 4-10 cm long, brownish at base, green-reddish in younger parts, flowering shoots contrast with their yellowish-green colour and a very sparse glandular hairy indumentum from the middle half upwards; leaf-scars croissant-shaped. Leaves of vegetative growth simple, decussate, fleshy, dark green to almost black (under shady conditions) or olive green (when exposed to the sun), subsessile to long petiolate; petioles 0.2-1.1(-3.3)cm long; laminas $3-5.2(-26) \times 0.3-1.5(-7)$ cm, narrowly to broadly lanceolate, bases obtuse, apices subacute, margins entire to bluntly sinuate; basal leaves of flowering shoots large, distinctly petiolate, with petioles up to 3 cm long and laminas up to 13 × 3.5 cm, broadly lanceolate, together with shoot mostly brighter coloured than vegetative growing parts; laminas and petioles towards inflorescence continuously more reduced until the leaves are almost filiform and sometimes appear conduplicate. Inflorescences a homocladic thyrsoid, after terminal flower once or twice dichasially ramified, then

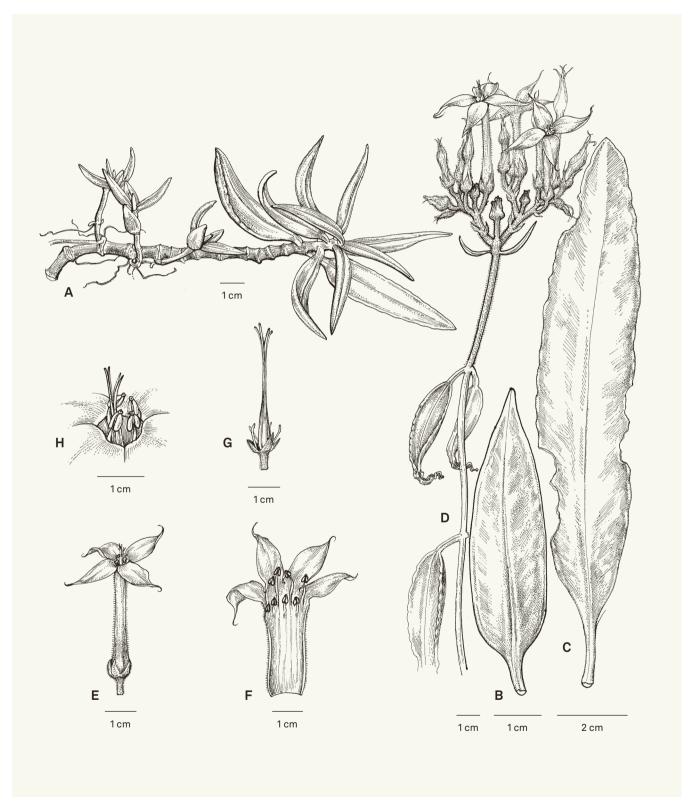


Fig. 2. — Kalanchoe luteola D.-P. Klein, Letsara & Mangelsdorff. A. Vegetative creeping habit during the dry season; B. Short-petiolate and small leaf; C. Distinctly petiolate, large leaf in creeping vegetative parts; D. Inflorescence on flowering shoot; E. Flower; F. Dissection of corolla, showing androecium; G. Gynoecium; H. Anthers of oppositipetalous whorl with anther connectives and styles protruding the tube. [Rodewald et al. SER 23-006, TAN] [Drawings: R.L. Andriamiarisoa]

continuing monochasially by forming 2-4 multiflorous erect cincinni (occasionally 1-2 pairs of partial inflorescences in the upper nodes below the main inflorescence), with up to 52 erect flowers; peduncles short, c. 0.5-4 cm long, occasionally bearing a singular plantlet at post-anthesis; bracts lanceolate, almost filiform, narrowing upwards, c. 3.3-3.5 × 0.15-0.2 cm; bracteoles similar to bracts in shape, 2.8-3.7 × 0.5 mm, densely covered with glandular hairs; pedicels 7–10 × 0.8–1.5 mm, bright green to greenish yellow, erect, densely covered with glandular hairs. Flowers erect, c. 35-45 mm long, creamy lemon yellow; sepals 3.7-4.7 × 1.3-1.9 mm, narrowly deltoid, apically acute, appressed to corolla in lower 34, abaxially densely glandular hairy, bright to dark green, fused only at base, forming an indistinct calyx tube 0.7-0.85 mm long; corolla tubes 25-43.5 mm long, ± quadrangular, 3-4.5 mm in diam. at its widest part, bright green to greenish yellow, abaxially moderately covered with glandular hairs 0.15-0.3 mm long; lobes 11.3–14.5 × 7–9 mm (including arista), abruptly spreading, ovate, tapering towards the apex with an arista 1.3-5.5 mm long, creamy lemon yellow, abaxially sparsely glandular hairy; androecia composed of 8 stamens, arranged in two whorls of 4, anthers of alternipetalous whorl included, anthers of oppositipetalous whorl exserted for 1-2 mm; alternipetalous filaments inserted at $\frac{9}{10}$ of the length of the corolla tube (c. 26–39.5 mm above the base), free for 1-2.5 mm, oppositipetalous filaments inserted at c. 30.5-41.5 mm above the base, free for 2.5-3.3 mm; anthers yellow, ovoid, each theca 1.3×0.35 mm, bases emarginate, apices rounded, with an orange-coloured globule; gynoecia with 4 oppositipetalous carpels, adherent in their lower ¾, forming ovaries c. 12 mm long, 1.9-2.2 mm in diam., only slightly wider than the styles; styles filamentous, c. 22-28 mm long, in older flowers protruding the corolla tube; nectar scales at base of carpels, linear with bifurcate apex, $8-11.5 \times 0.3$ mm at apex (0.6 mm at base), thin, whitetransparent. Seeds $0.7-0.8 \times 0.2-0.3$ mm, brown, testa tesselate.

Distribution, ecology and phenology. — Kalanchoe luteola is known only from a single population in the Tsingy de Bemaraha National Park, in the vicinity of Bekopaka, western Madagascar (Fig. 1). It grows in shallow humus-filled crevices and depressions of jurassic limestone (Goodman et al., 2018), very localised in the more exposed parts of the tsingy (Fig. 3A). The most frequently recorded species occurring along with the new species include Commiphora sp. (Burseraceae), Cynanchum sp. (Apocynaceae), Euphorbia viguieri Denis (Euphorbiaceae), Kalanchoe bogneri Rauh (Crassulaceae), Orchidaceae (several species), Pachypodium menabeum Leandri, and P. rosulatum subsp. bemarahense Lüthy & Lavranos (Apocynaceae).

Kalanchoe luteola was found flowering in June and fruiting in September.

Conservation status. – Although Kalanchoe luteola occurs within the protected Tsingy de Bemaraha National Park on outcrops difficult to access, the taxon consists of a very small population, estimated to 150–200 individuals seen in situ, within a very restricted area of occupancy estimated to be less than 20 km². Despite its protection, the Tsingy de Bemaraha forests are threatened and subject to wild fires (GOODMAN et al., 2018). Due to plausible threats on its habitat, the risk of extinction of Kalanchoe luteola is therefore preliminarily assessed as "Vulnerable" [VU D2] in accordance with IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. - Kalanchoe luteola is a typical representative of the subgenus Kalanchoe native to Madagascar (Klein et al., 2021); it is a plant partially covered with a glandular indumentum, which has erect flowers with an indistinct calvx tube, filaments inserted above the middle of the corolla tube, anthers that are either included or only very slightly exserted from the tube, spherical connective glands on their apices, and linear nectar scales. However, while in most representatives of this subgenus the styles are much shorter than the ovaries or equal in length (Descoings, 2006), K. luteola possesses styles much longer than the ovaries (see Table 1). Kalanchoe luteola is most similar to the other three known species with yellow flowers of subg. Kalanchoe from western Madagascar, i.e., K. antennifera, K. boisii and K. chapototii Raym.-Hamet & H. Perrier. These species share erect, yellow to orange flowers that are glandular hairy on their outer parts, long corolla tubes, globules on the apices of their anthers, and long aristate appendages on their petal lobes (Fig. 3). Kalanchoe luteola differs from these species by its life cycle, the shape of its leaves, the absence of an indumentum in the vegetative stage, and by the length of its corolla tube (RAYMOND-HAMET & PERRIER DE LA BÂTHIE, 1914, 1915; Descoings, 2004; Table 1). The new species stands out among all other Kalanchoe species from Madagascar for having the longest known corolla tube, followed by that of K. tuberosa H. Perrier. Its particularly long corolla tube additionally shows great resemblance to species of this subgenus from the African continent, such as K. latisepala N.E. Br. (native to Malawi and Mozambique) or K. marmorata Baker (native to central and east Africa).

During the vegetative growth, the leaves of *Kalanchoe luteola* show a clear transformation between those formed during the rainy season (distinctly petiolate, large, broadly lanceolate) and those formed during the dry season (sessile, small, narrowly lanceolate) and this transformation is still recognisable during the flowering period by wilting leaves that are still attached to the plant. This adaptation to seasonally strongly varying conditions is known from other species such as *K. boisii* and *K. humifica*. These three species, besides their ontogenically variable vegetative stage coloration peaking in very dark greens, exhibit nearly identical leaf shape transitions,

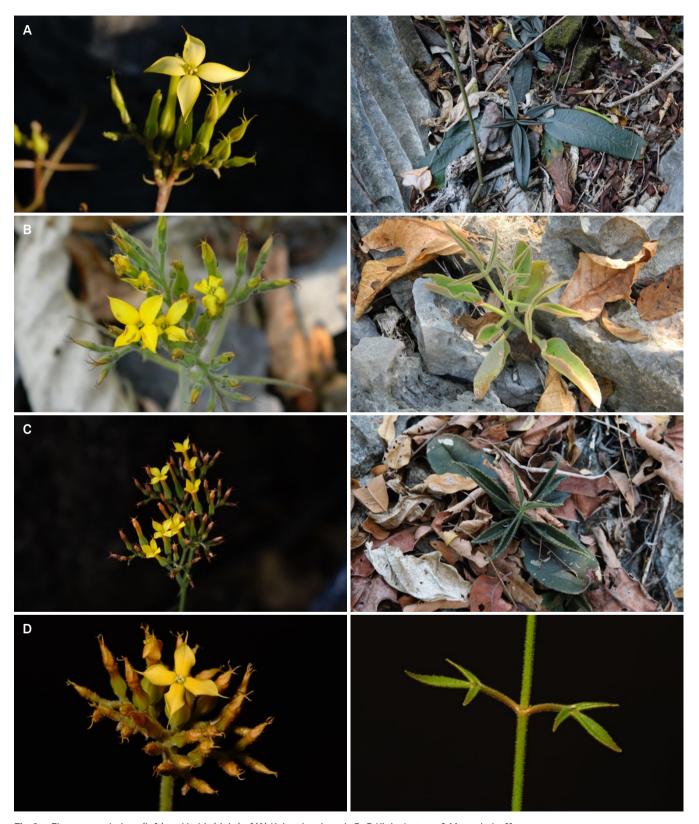


Fig. 3. – Flower morphology (left) and habit (right) of (A) Kalanchoe luteola D.-P. Klein, Letsara & Mangelsdorff; (B) K. chapototii Raym.-Hamet & H. Perrier; (C) K. boisii Raym.-Hamet & H. Perrier; (D) K. antennifera Desc. [Photos: A, C, D: D.-P. Klein; B: R. Letsara]

and can easily be confused at certain stages of vegetative development. Such similarities in coloration and leaf shape during ontogenic development may result from convergence due to similar environmental conditions.

Kalanchoe manambolensis D.-P. Klein, Letsara & Shtein, sp. nov. (Fig. 4).

Holotypus: MADAGASCAR. Reg. Melaky [Prov. Mahajanga]: Bekopaka, Tsingy de Bemaraha, [19°08'S 44°49'E], 65 m, 21.IX.2023, Rodewald, Shtein, Letsara & Tsiverilaza SER 23-002 (TAN!; iso-: G!, M [M-0356644]!).

Kalanchoe manambolensis D.-P. Klein, Letsara & Shtein is distinguished from other Malagasy Kalanchoe species by having omnidirectional, slightly zygomorphic flowers with a calyx tube being almost twice as long as the sepal lobes, somewhat 4-angled, and appressed to the corolla only in the lower ½. It can be distinguished from K. aromatica H. Perrier by having corolla lobes much shorter than the tube, and by the stamens only very slightly protruding from the corolla tube. It can be further distinguished from K. bouvetii Raym.-Hamet & H. Perrier by its bigger stature, and by having a much shorter corolla tube with petal lobes that are fully recurved.

Plants medium-sized succulent herbs, up to 60 cm tall, sparsely to densely covered with a hairy indumentum on all parts, except fertile parts of the flower (carpels, stamens) and adaxial side of petals; slightly aromatic e.g. on leaves. Stems up to 44 cm long, basally woody, bearing up to 7 pairs of leaves, generally unbranched, sprouting only basally, densely covered with an indumentum of simple, c. 0.3–0.6 mm long, transparent and brownish hairs. Leaves simple, recumbent to spreading,

bright to dark green, sessile to shortly-petiolate, petioles broad, $0.2-1.5 \times 0.3-0.6$ cm, laminas up to 17.5×5.5 cm, broadly lanceolate, bases attenuate to rarely obtuse, apices subacute, adaxially canaliculate for 3/3 of its length, margins irregularly smoothly crenate to dentate, partially with purple spots, on both sides covered with a dense indumentum of simple, c. 0.3 mm long, simple hairs. Inflorescence a paniculate, heterocladic thyrsoid producing cincinnate partial inflorescences from up to five nodes below the terminal flower, carrying altogether c. 70 flowers, whereby the more basal partial inflorescences produce increasingly longer peduncles; peduncles c. 2.5 cm; bracts sessile, oblanceolate, apices acute, margins irregularly dentate, 18.9-33.1 × 5.5-11.1 mm, thin-fleshy and bright green, on both sides covered with a dense indumentum of simple, ca. 0.3 mm long, transparent hairs; bracteoles sessile, lanceolate, apices acute, margins entire, 2.1–4.4 × 0.4–1.1 mm, very thin and nearly transparent, on both sides densely covered with a viscid indumentum of glandular, c. 0.3 mm long, transparent hairs; pedicels 3.0-7.5 × 0.75-1.0 mm, slightly widening towards the flower, sparsely covered with a viscid indumentum of glandular, c. 0.3 mm long, transparent hairs. Flowers omnidirectional, slightly zygomorphic, c. 18 mm long; sepals green, forming a distinct tube of 6.1-6.6 × 4.1-5.4 mm; sepal lobes much shorter than calyx tube, 3.8-4.2 mm long, deltoid, apically acute; corolla tubes 10.7–10.8 mm long, suburceolate, 2.1-3.0 mm in diam. at its widest part, white-greenish, abaxially sparsely to moderately covered with a viscid indumentum of glandular, c. 0.1-0.2 mm long, transparent hairs; lobes $3.3-3.5 \times 2.4-2.6$ mm (including mucro), broadly obovate, mucronate, mucro 0.3 mm long, fully recurved, adaxially white with broad pink stripes, glabrous, abaxially whitish-green, sparsely to moderately covered with a viscid indumentum of

Table 1. – Diagnostic characters distinguishing *Kalanchoe luteola* D.-P. Klein, Letsara & Mangelsdorff from *K. antennifera* Desc., *K. boisii* Raym.-Hamet & H. Perrier, and *K. chapototii* Raym.-Hamet & H. Perrier.
[1: RAYMOND-HAMET & PERRIER DE LA BÂTHIE (1915); 2: RAYMOND-HAMET & PERRIER DE LA BÂTHIE (1914); 3: DESCOINGS (2004); 4: in vivo observations]

	K. luteola	K. chapototii	K. boisii	K. antennifera
Habit height [cm]	78 (incl. inflorescence)	28-44 [1]	13.5-27(-180) (incl. inflorescence) [2, 4]	10-20 [3]
Life cycle	perennial	annual [1]	annual [2]	annual [3]
Indumentum	glabrous except for flowering shoot and inflorescences	completely covered with a glandular indumentum [1, 4]	completely covered with a glandular indumentum [2, 4]	completely covered with a glandular indumentum [3, 4]
Leaves	simple	tri-to 5-partite [1, 4]	simple to tri-partite [2, 4]	simple to tri-partite [3, 4]
Length of corolla tube without petal lobes [mm]	25-43.5	19.5–21.8 [1]	12-13 [2]	11–12 [3]
Length of ovary [mm]	c. 12	7.9-11.4 [1]	3.7-8.6 [2, 4]	5.8-8 [3, 4]
Length of style [mm]	22-28	15.6–18 [1]	2.5-2.8 [2, 4]	2.1-4 [3, 4]
Colour of petal lobes	creamy yellow	pale to bright yellow [1, 4]	golden yellow to orange [2, 4]	golden yellow to orange [3, 4]

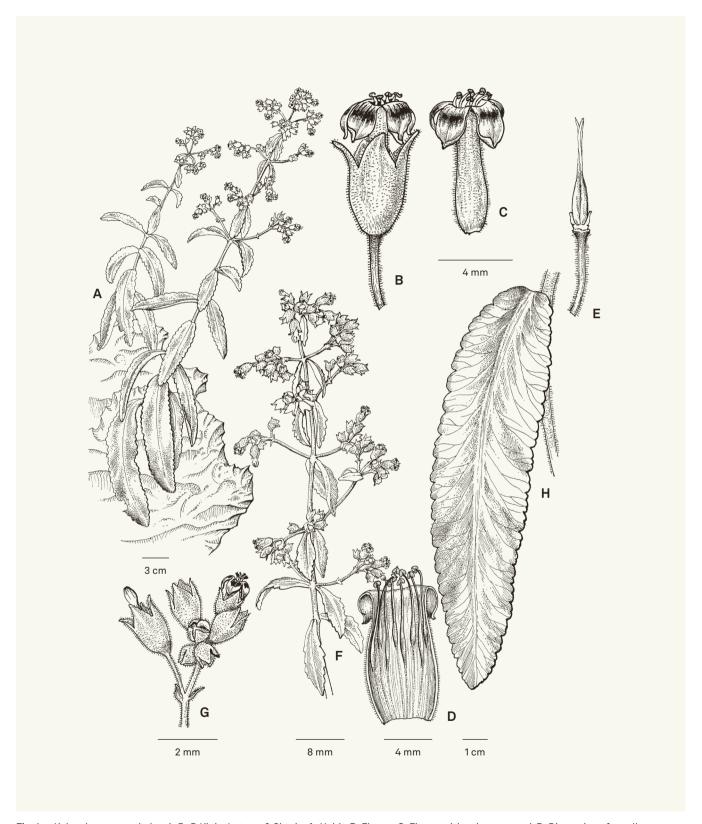


Fig. 4. – Kalanchoe manambolensis D.-P. Klein, Letsara & Shtein. A. Habit; B. Flower; C. Flower with calyx removed; D. Dissection of corolla, showing androecium; E. Gynoecium; F. Inflorescence on flowering shoot; G. Single inflorescence; H. Sessile leaf during flowering season. [Rodewald et al. SER 23-002, TAN] [Drawings: R.L. Andriamiarisoa]



Fig. 5. – Flower morphology (left) and habit (right) of (A) *Kalanchoe manambolensis* D.-P. Klein, Letsara & Shtein; (B) *K. aromatica* var. *aromatica* H. Perrier; (C) white flowered form of *K. bouvetii* Raym.-Hamet & H. Perrier. [Photos: A, B: D.-P. Klein; C: A. Hankey]

glandular, c. 0.1–0.2 mm long hairs; androecia composed of 8 stamens, arranged in two whorls of 4, anthers of alternipetalous whorl exserted for c. 0.5 mm, anthers of oppositipetalous whorl exserted for c. 1.5 mm; lower filaments alternipetalous, inserted at c. 4.0-4.5 mm above the base of the corolla tube, free for 6.7–7.5 mm, upper filaments oppositipetalous, inserted at c. 6 mm, free for 6.5-8.5 mm; anthers violet when young, light brownish at anthesis, with a small transparent globule on the apex; gynoecia composed of 4 oppositipetalous carpels, adherent in their lower half, forming ovaries c. 5.4-5.5 mm long, together reaching a diameter of 1.5-1.6 mm at their broadest point; styles free for all of their length, filamentous, 4-6.8 mm long; nectar scales strap-shaped with bifurcate apex, $1.4-1.9 \times 0.3-0.7$ mm, thin, white-transparent, slightly appressed to carpels. Seeds $0.6-0.7 \times 0.2-0.3$ mm, brown, striate.

Distribution, ecology and phenology. – Kalanchoe manambolensis is known only from a single population in the Parc National de Tsingy de Bemaraha National Park, in the vicinity of Bekopaka in western Madagascar, where it grows along with *Aloe bosseri* J.-B. Castillon (*Asphodelaceae*), *K. berevoensis* Rebmann, and *Kalanchoe boisii* Raym.-Hamet & H. Perrier (*Crassulaceae*) near and on cliffs above the banks of the Manambolo river (Fig. 1, 5A).

The new species flowers in June, where it was observed being visited by the bee *Amegilla antimena* (Saussure, 1890) (*Apidae*); fruiting plants were collected in September.

Conservation status. – Although Kalanchoe manambolensis occurs within the protected Tsingy de Bemaraha National Park partially on outcrops difficult to access, the new species is known from a small population, estimated to 500–1,000 individuals seen in situ, within a very restricted area of occupancy estimated to be less than 20 km². Despite its protection, the Tsingy de Bemaraha forests are threatened and subject to wild fires (Goodman et al., 2018). Due to plausible threats on its habitat, the risk of extinction of K. manambolensis is therefore preliminarily assessed as "Vulnerable" [VU D2] in accordance with IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – Kalanchoe manambolensis is morphologically most similar to K. aromatica, for which two varieties are described, and K. bouvetii (Table 2). The morphological affinity of the latter two species is supported by a recently published molecular phylogenetic analysis of the genus that shows a sister relationship between K. aromatica and K. bouvetii (Rodewald et al., 2025). All three species share a small to medium sized habit, omnidirectional flowers with distinct, often zygomorphic corolla tubes, and are at least partially covered by glandular trichomes (Fig. 5). Kalanchoe manambolensis can be distinguished from K. aromatica var. aromatica by having

an indumentum that is glandular only in the inflorescence, strictly simple leaves, sessile to shortly-petiolate leaves, petal lobe/corolla tube ratio being much shorter, colour of the petal lobes being white with red-pink stripes, and by the stamens only very slightly exserted from the corolla tube. It differs from K. aromatica var. brevicorolla Boiteau by being a larger plant and by having larger flowers with a longer corolla tube, a greenish carpel, and whitish styles. Kalanchoe manambolensis can be further distinguished from K. bouvetii by the larger stature, by having a much shorter corolla tube, that is only very slightly zygomorphic, and petal lobes fully recurved. Both species share the non-glandular hairs on vegetative parts that are partially glandular in most generative parts. They also share the following characters: simple leaves, sepal lobes shorter than the calyx tube, stamens only very slightly exserted from the corolla tube, and presence of a globule on the apices of the anthers. The latter is a feature otherwise only seen in species of Kalanchoe subg. Kalanchoe.

Based on herbarium specimens of *Kalanchoe aromatica* and *K. bouvetii*, as well as material that cannot be clearly assigned to either one (here provisionally treated as *K.* aff. *bouvetii*), the distribution range of these related species (including *K. manambolensis*) extends from the western part (Tsingy de Bemaraha National Park, New Protected Area of Analavelona, and Isalo National Park), to the central part (High Plateau, Kelifely) and presumably to the northern part of Madagascar (Montagne d'Ambre National Park). The presently known disjunct distribution of taxa of this complex can be explained, among other reasons, by the high degree of destruction of the natural ecosystems between the areas of occurrence and the generally low level of scientific collecting activity in non-protected areas.

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Table 2. – Diagnostic characters distinguishing K. manambolensis D.-P. Klein, Letsara & Shtein from K. aromatica var. aromatica H. Perrier, K. aromatica var. brevicorolla Boiteau, and K. bouvetii Raym.-Hamet & H. Perrier.

[1: Perrier de la Bâthie (1923); 2: Boiteau & Allorge-Boiteau (1995); 3: Raymond-Hamet & Perrier de la Bâthie (1914); 4: in vivo observations]

	K. manambolensis	K. aromatica var. aromatica	K. aromatica var. brevicorolla	K. bouvetii
Habit height [cm]	60 (incl. inflorescence)	30-60 [1]	much smaller than var. aromatica [2]	14-42 [3]
Indumentum	sparsely to densely covered with transparent, simple (stem and leaves) and glandular (inflorescence) hairs	densely covered with long capitate glandular hairs with a red tip [1, 4]	, no information available	during vegetative growth covered with long, simple hairs; flowering stems covered simultaneously with long, simple hairs and short, glandular hairs [3]
Leaves	simple	simple to tripartite [1]	simple [2]	simple [3]
Leaf margins	smoothly crenate to dentate with purple spots	undulate, serrate-dentate with red margins and purple spots [1, 4]	dentate [2]	crenate to sinuate with brown spots [3]
Leaf orientation	decumbent to spreading	spreading to erect [1,4]	no information available	spreading to erect [4]
Petiole	sessile to barely petiolate (up to 15 mm long)	petiolate (up to 30 mm long) [4]	no information available	shortly-petiolate (up to 6 mm long) [3]
Length of corolla tube [mm]	10.7–10.8	6.5-8 [1]	c. 6 [2]	11.6-22.5 [3]
Length of petal lobes [mm]	3.3-3.5	slightly shorter than corolla tube [1]	no information available	2.9-5.2 [3]
Petal lobe/corolla tube ratio	much shorter	about as long	no information available	much shorter
Length of calyx tube [mm]	6.1-6.6	4-5 mm [1]	slightly shorter than var. aromatica [2]	3.7-5.2 [3]
Length of sepal lobes [mm]	3.8-4.2	slightly shorter than calyx tube [1]	c.1[2]	2.2-3.2 [3]
Sepal lobe/calyx tube ratio	shorter	about as long	much shorter	shorter
Colour of carpel	green	green [1, 4]	reddish [2]	green [4]
Colour of styles	whitish	whitish [1, 4]	reddish [2]	whitish [4]
Colour of petal lobes	white with red-pink stripes	greenish-white with dark red to blackish stripes [1, 4]	white with red-pink stripes [2]	white to pale purple, sometimes with purple stripes [3, 4]
Stamens exerted	somewhat	strongly [1,4]	no information available	somewhat [4]

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