



Petalidium saxatile (Acanthaceae), a new species from Namibia

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Abstract

Petalidium saxatile, hitherto confused with *P. canescens*, and the widespread *P. setosum*, is here described as a new species. It is a range-restricted species, only known from the vicinity of Palmwag and southwards to the Bergsig area with an outlier population to the south of Khorixas in the Kaokoveld Centre of Endemism, northwestern Namibia. It grows mainly among basaltic rocks of the Etendeka Group on arid hillsides and along ephemeral riverbeds and drainage lines. Diagnostic characters for *P. saxatile* include the pale green appearance of the plants, vegetative parts with a dense white indumentum of relatively short dendritic trichomes appearing matted on young leaves, flowers borne in compact dichasia, and long simple eglandular trichomes on the bracts visible to the naked eye. The flowers of *P. saxatile* are distinctive in having the corolla lobes inside (adaxially) distinctly bicolorous: the upper and lateral lobes are pink or brown-pink, while the anterior lobe is yellow. Additionally, all lobes are discolorous in being much paler outside (abaxially). Furthermore, analyses of genetic data across many nuclear loci, generated using a ddRADseq approach, show the species to be genetically distinct from *P. canescens*. A comparison of key morphological features distinguishing *P. saxatile* from *P. canescens* and *P. setosum*, is provided. Based on IUCN Red List criteria, a provisional conservation assessment of Endangered (EN) is recommended for the new species. It is suggested that the Etendeka Tableland, to which *P. saxatile* is largely confined, may serve as a local subcentre of plant endemism within the larger Kaokoveld Centre of Endemism, at least for species in the genus *Petalidium*.

Key words: Bergsig, endemism, Etendeka Group, flora, genetics, Kaokoveld Centre of Endemism, Khorixas, Kunene Region, *Oberholzeria*, Palmwag, RADseq, Ruellieae, taxonomy

Introduction

Currently, 43 species of *Petalidium* Nees von Esenbeck (1832: 75) are recognised in Africa. The primary centre of diversity for this genus is located in northwestern Namibia and neighbouring southwestern Angola. Namibia is home to 33 species, while 13 species are recorded in Angola, six in South Africa, and a total of 35 species are noted in the *Flora of southern Africa region*, which includes South Africa, Namibia, Botswana, Eswatini, and Lesotho (Germishuizen & Meyer 2003, Figueiredo & Smith 2008, Swanepoel 2020, Swanepoel & Manzitto-Tripp 2022, Swanepoel *et al.* 2022, Dexter *et al.* 2023, Swanepoel & Van Wyk 2023a, b, Swanepoel *et al.* 2023, 2024).

As of now, there is no up-to-date published key available for identifying all the accepted species of *Petalidium*. This paper forms part of a long-term project, led by one of us (WS), aimed at conducting extensive fieldwork on *Petalidium* in botanically underexplored regions, particularly in Namibia and Angola. The objective is to discover

and document any remaining unidentified or undescribed species of the genus. The ultimate goal is to produce a comprehensive monograph of *Petalidium*, a significant undertaking that will require considerable time to complete. Given the time, cost, and effort associated with fieldwork, we have adopted the approach of formally describing new taxa as they are discovered, in order to justify the ongoing investment in exploration.

In the present contribution a new species of *Petalidium* is described. According to available distribution records, this new entity is restricted to the Namibian part of the Kaokoveld Centre of Endemism—a biogeographical region rich in range-restricted plant species in northwestern Namibia and adjacent southwestern Angola (Van Wyk & Smith 2001).

During a botanical expedition to the Palmwag area in May 2018, one of us (WS) encountered an unfamiliar *Petalidium* characterised by its dwarf shrub habit, multi-stemmed from just below or above ground level, green leaves and vegetative parts with relatively short dendritic trichomes, and flowers in compact dichasia becoming woody with age. The plants were in flower, enabling the taxon to be tentatively identified as an undescribed species. In May 2022 the taxon was also encountered by another one of us (KGD) in this same area and independently recognized as a potentially undescribed species. Similar plants were subsequently collected from near Bergsig as well. The new species can be confused with several other members of *Petalidium* in northwestern Namibia with which it shares morphological similarities, especially in features of the habit, indumentum, leaves, and flowers. Its morphologically most similar congeners are *P. canescens* Clarke (1899: 92) (especially the narrow-leaved form) and *P. setosum* Schinz (1916: 434). A study of the *Petalidium* holdings in the Herbs PRE, PRU, and WIND revealed several earlier collections of the new species, all filed either under *P. canescens* or *P. setosum*. To confirm the genetic distinctness of the putative new species, we generated data from 1317 SNPs via a ddRADseq pipeline that has previously been used in *Petalidium* to elucidate species relationships (Tripp *et al.* 2017, Loiseau *et al.* 2023). We sequenced multiple individuals of the putative new species, as well as diverse species growing nearby in the Kaokoveld Centre of Endemism.

The Kaokoveld Centre is a pronounced centre of diversity and endemism for *Petalidium* (Craven 2009, Tripp *et al.* 2017, Dexter *et al.* 2023, Loiseau *et al.* 2023) and related Acanthaceae (e.g., Tripp & Dexter 2012, Darbyshire *et al.* 2020). The Centre is still botanically underexplored, hence the identification of yet another new species in this region is not unexpected.

Methods

Morphological descriptions and ecological information presented here are based primarily on field observations and material collected following extensive field work in Namibia. Diagnostic features for the new species, *P. canescens*, and *P. setosum* were determined through examination of fresh material, the type material in Herb. WIND, as well as high-resolution images of type material available on JSTOR Global Plants (<https://plants.jstor.org/>). This was supplemented by the study of the protologues and available herbarium collections in the National Botanical Research Institute in Namibia (WIND), the South African National Biodiversity Institute, Pretoria (PRE), and the University of Pretoria (PRU) (herbarium codes follow Thiers 2024). A 6.5–45.0× magnification stereo microscope was used for studying morphological features. Descriptive terminology follows Beentje (2016), Manktelow (2000), and Hewson (2019). Locality information for specimens cited also provides the quarter degree grid squares following the degree reference system of Edwards & Leistner (1971). The distribution map was compiled from specimen data using ArcView 3.1 software. A preliminary conservation assessment was conducted using the standard procedures based on IUCN (2012) categories and criteria, and the online GeoCAT tool (Bachman *et al.* 2011).

To assess the genetic distinctness of this new species, we generated ddRADseq data, following protocols used in previous phylogenetic work on the genus *Petalidium* (Tripp *et al.* 2017, Loiseau *et al.* 2023), which are briefly summarised here. DNA was extracted from silica-dried leaf tissue using a CTAB bench protocol (Doyle & Doyle 1987). We used EcoR1 and Mse1 for double digestion, followed by size selection of 250–500 bp fragments. Libraries were sequenced at the University of Liverpool Centre for Genomics Research on an Illumina Novaseq 6000.

Sequenced libraries were demultiplexed and reads were checked by quality, including adapter trimming and base quality filtering, using the software ipyrad (Eaton & Overcast 2020). This software is commonly used as an assembly and analysis toolkit for restriction-site associated DNA (RADseq) data. We used the default parameters for both demultiplexing and SNPs calling steps, by allowing the formation of 0.90 identity clusters for sequence similarity and 1 mismatch in the barcodes. Reads were aligned to the *Petalidium crispum* Meyer (1961: 66) reference genome (Manzitto-Tripp *et al.*, unpubl. data). We included six individuals of the putative new species, 12 individuals of *P.*

canescens, and one individual each of 13 other species that occur in the Kaokoveld Centre of Endemism. We included an individual of *Barleria* Linnaeus (1753: 636) (Acanthaceae) as an outgroup.



FIGURE 1. *Petalidium saxatile*, habitat and habit. Note relatively narrow leaves ca. folded upwards along the midrib (B & C). **A.** Several plants (some arrowed) growing in typical habitat among stones comprising Etendeka Group basalt on an arid hillside. **B.** Plant with pale grey-green foliage due to a more persistent whitish indumentum, and inflorescences. **C.** Plant in flower and with greenish foliage resulting from a sparser indumentum. Photographs by W. Swanepoel.

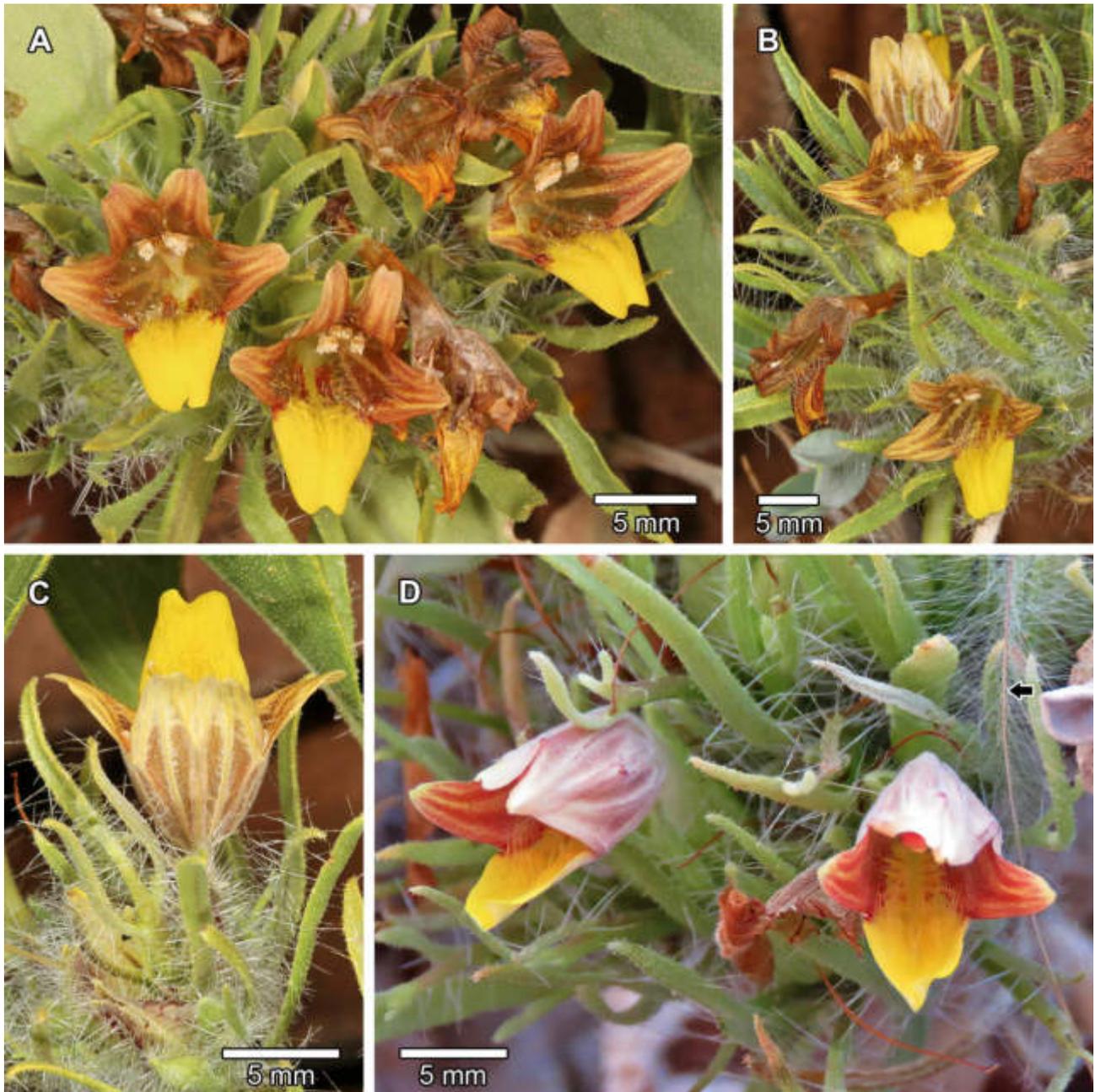


FIGURE 2. *Petalidium saxatile*, morphology of flowers. **A, B.** Newly opened and faded flowers. Anterior corolla lobe inside (adaxially) bright yellow and without nectar guides. **C.** Flower viewed from above, showing puberulous abaxial surface of posterior corolla lobes. **D.** Flowers viewed obliquely from above, all corolla lobes discolorous with the outside (abaxial) surfaces puberulous and notably paler in colour. The long white trichomes next to the flower on the right do not belong to the plant, but is a wind-blown feathery awn (arrowed) of a member of the grass genus *Stipagrostis*. Photographs by W. Swanepoel.

For phylogenetic inference, we employed two different methods. We created a phylogeny based on Maximum Likelihood (ML) using the RaxML GUI v2.0.13 (Stamatakis 2014). We obtained a second phylogenetic tree by bayesian inference (BI) with mrBayes v3.2.7a (Ronquist *et al.* 2012). In both cases we used a GTR+I model of evolution, which was determined to be most probable with JModelTest2 (Darriba *et al.* 2012). In the case of ML we assessed the accuracy using a bootstrap ($n = 1000$) approach, while in the case of BI we built 1.5×10^6 trees including an initial burn-in of the 10%.

To examine reticulation among species, and test for a potential hybrid origin of the new species, we created a Neighbour-net with SplitsTree v6.3.40 (Huson 1998). Splits support was assessed by 1000 bootstrap replicates. For this analysis, we excluded *P. luteoalbum* Meeuse (1960: 409), *P. giessii* Meyer (1967: 507), and *Barleria*, which the phylogenetic analysis showed to be basally diverged from the clade in which the new species sits.

All ddRAD libraries are available on GenBank under the Sequence Read Archive Study SUB12441993. Our data are tagged as biosamples from SAMN45187462 to SAMN45187492.

Taxonomic treatment

Petalidium saxatile Swanepoel, K.G.Dexter, E.Tripp & A.E.van Wyk, *sp. nov.* (Figs 1–3)

Diagnosis:—A woody dwarf shrub up to 0.5 m tall, morphologically most similar to *Petalidium canescens* and *P. setosum*, differing by having indumentum on vegetative parts consisting of simple (weak and robust), bifurcate, stellate-dendritic, dendritic and stalked glandular trichomes, lacking sessile glands (*vs.* indumentum strigose with in addition widely spaced long, robust, simple trichomes [*P. canescens*]; long, robust, simple and stalked glandular trichomes, sessile glands present [*P. setosum*]); leaf lamina conduplicate (*vs.* flat or subconduplicate [*P. canescens*]; flat or irregularly curved, twisted, widely undulate, recurved or incurved towards margins [*P. setosum*]), usually narrower, up to 22 mm wide (*vs.* up to 100 mm [*P. canescens* (broad-leaved form)]; up to 50 mm [*P. setosum*]), with 3 or 4 principal lateral veins each side (*vs.* 4–6 [*P. canescens*]; 3–7 [*P. setosum*]); corolla expanded portion longer, 7.7–9.1 mm long (*vs.* ca. 7.5 mm [*P. canescens*]; ca. 3.4 mm [*P. setosum*]), anterior lobe inside (adaxially) bright yellow, lateral and upper lobes pink or brown-pink, darker towards bases (*vs.* all lobes similarly coloured: violet-red but anterior lobe darker [*P. canescens*]; purple, burgundy or carmine, anterior lobe sometimes yellow towards apex [*P. setosum*]), nectar guides absent (*vs.* present).

Type:—NAMIBIA. Kunene Region: Farm Driefontein 716, ca. 8 km south-southwest of homestead, southern tributary to Springbok River, rocky area above river bed, 2013BD, 869 m a.s.l., 20 March 2022, *Swanepoel 645* (holotype WIND!; isotypes PRE!, PRU!).

Hemispherical woody dwarf shrub up to 0.5 m tall; all vegetative parts with sparse to matted white indumentum, trichomes short, eglandular, simple, bifurcate, stellate-dendritic and sparsely branched dendritic with branches tapering, also with longer bottlebrush-like dendritic ones and widely-spaced more robust, longer, stalked glandular trichomes and much longer robust multi-cellular bulbous-based simple, eglandular trichomes up to 3 mm long in addition. *Stems* single or multi-stemmed from just below or above ground level, erect to procumbent, older distal stems cylindrical, bark smooth or longitudinally fissured and peeling in long narrow strips, cream- or grey-white; young stems quadrangular, green, glabrescent, cystoliths visible, linear, linear-oblongate or narrowly elliptic. *Leaves* opposite and decussate on new shoots, fascicled on older stems; petiole 1–18 mm long; lamina ovate, lanceolate [*sensu* Lindley's definition (Beentje 2016)] or elliptic, conduplicate, 13–70 × 4–22 mm, green to grey-green (due to white indumentum), apex acute or obtuse, base attenuate or cuneate, margins entire, midrib and the 3 or 4 principal lateral veins prominently raised adaxially, longer robust multi-cellular bulbous-based simple trichomes sometimes absent, cystoliths visible adaxially, linear. *Flowers* in axillary compact dichasia with sterile branches; bracts foliaceous, linear, linear-lanceolate [*sensu* Lindley's definition (Beentje 2016)] or linear-oblongate, sessile, 19.0–25.0 × 0.8–3.5 mm, indumentum similar to vegetative parts but trichomes scattered (not matted), long robust multi-cellular bulbous-based simple trichomes mostly on margins; pedicels (below bracteoles; “peduncle” of some authors) up to 1 mm long; bracteoles narrowly ovate, symmetrical, papery, ca. 10.7 × 4.4 mm, apex attenuate, pale green or green, stramineous when dry, venation reticulate, dark green, abaxially with indumentum of scattered short simple trichomes and small, short-stalked glandular ones towards apex with in addition long robust multi-cellular bulbous-based simple trichomes, otherwise glabrous, adaxially sparsely strigose towards apex, otherwise glabrous, margin lanate towards apex, cystoliths visible both sides, small, linear, dense. *Calyx* ca. 8.4 mm long including basal tube of ca. 1.0 mm deep, lobes 4, regular, narrowly triangular, acute, unequal, 6.6–7.4 × 0.8–1.5 mm, anticous lobe bifid for ca. 1.1 mm; strigose both sides. *Corolla* with narrow unexpanded portion of tube cylindrical, laterally slightly flattened, 23.3–26.5 mm long with lobes straightened, narrow portion 10.0–13.3 mm long, 1.8–2.3 mm diam., outside glabrous, inside puberulous distally on anterior side otherwise glabrous, expanded portion at slight angle to anterior side of narrow portion, 7.7–9.1 mm long, outside puberulous, inside of anterior part with scattered long stiff white simple trichomes towards mouth, inside otherwise glabrous, herringbone pattern prominently transversely 6-ribbed inside; lobes ascending-spreading or in same plane with respect to corolla tube axis, sometimes recurved towards apex, anterior lobe tapering, obovate or rectangular, apex emarginate, 6.5–7.1 × 4.3–5.6 mm, lateral and upper lobes tapering or ovate, apices rounded, lateral lobes 5.8–6.4 × 3.9 mm, upper lobes 6.7–7.0 × 2.9–3.6 mm, connate for 35–40% of their length, lobe margins entire or recurved towards apex, anterior lobe bright yellow inside (adaxially), lacking nectar guides, lateral and upper lobes pink or brown-pink, darker towards bases with traces conspicuous, paler than associated lobes, all lobes discolorous, outside (abaxially) much paler, glabrous inside (adaxially) except for few long stiff white simple trichomes towards

bases. *Stamens* didynamous, inserted dorsally in throat, fused portion ca. 1.7 mm long, free parts slightly tapering towards apex, glabrous, long filaments ca. 6.2 mm long, short filaments ca. 4.7 mm long, outer filament with basal ridge from point of insertion on corolla (“trace”) decurrent to ca. 9 mm from base of tube, puberulous; filament curtain reduced (*sensu* terminology of Manktelow 2000); anthers 2-thecous, thecae oblong, equal, ca. 3 mm long excluding short basal spur, pink-white with few to scattered small, stalked glandular trichomes towards apex. *Gynoecium* 17.0–20.5 mm long; ovary ovoid, laterally compressed, ca. 1.6 × 1.3 mm, inserted in fleshy disc, glabrous; style filiform, 15.0–18.6 mm long, puberulous, stigma lobes linear, unequal, longer lobe ca. 1.2 mm long, shorter lobe ca. 0.6 mm long. *Capsule* flattened ovoid, ca. 8 × 4 mm, tawny, glossy, glabrous; seeds cordate, ca. 3.7–4.2 × 2.8–3.0 mm, densely covered with white hygroscopic trichomes.

Phenology:—Flowers and fruit have been recorded from March to June (late summer to winter).

Distribution and habitat:—At present, *Petalidium saxatile* is only known from the Kaokoveld, northwestern Namibia, in the vicinity of Palmwag and southwards to the Bergsig area, with an outlier population on the farm Welbedacht to the south of Khorixas (Fig. 3). *Petalidium saxatile* occurs in rocky areas and among stones comprising Etendeka Group basalt (Milner *et al.* 1994) on arid hillsides and along drainage lines at elevations of 860–1130 m a.s.l., 70–150 km inland from the Atlantic Ocean. Average annual rainfall in the area is from less than 100 to 200 mm and falls in summer (Atlas of Namibia Team 2022). For other species of *Petalidium* mainly associated with substrates derived from Etendeka Group basalt, see under “Notes” below.

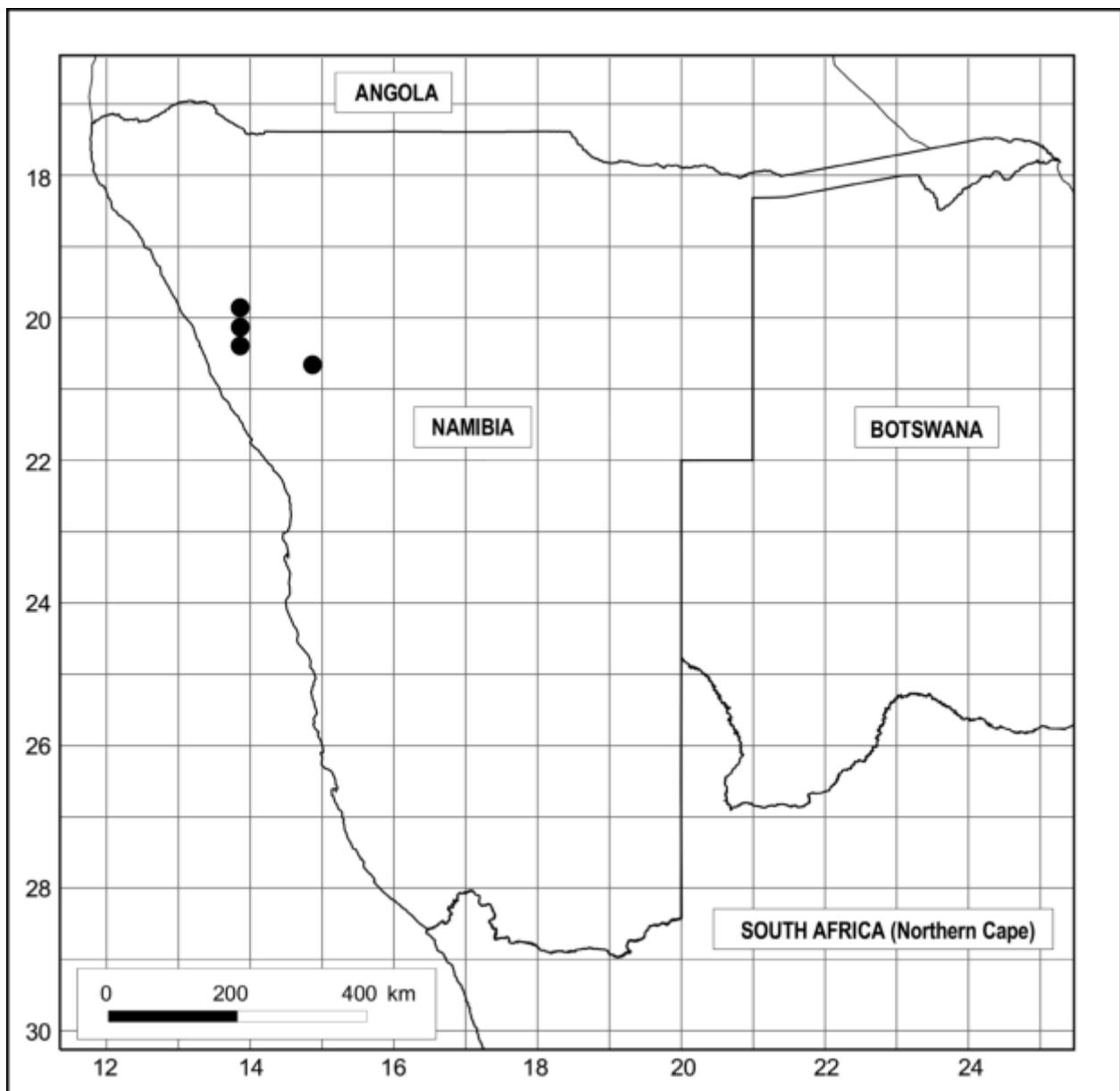


FIGURE 3. Known distribution of *Petalidium saxatile* (black dots). Based on herbarium specimens in Herbs. PRE, PRU, and WIND.

Conservation status:—*Petalidium saxatile* has been recorded at four localities in the vicinity of Palmwag and Bergsig and at one outlier locality represented by the gathering *Liebenberg 4954* (see note under “Additional specimens examined”) where it is occasional to locally common. Although a brief search at various other localities with seemingly suitable habitat did not reveal any plants, it is probably more widespread than currently known. The extent of occurrence (EOO) has been calculated as 3337 km² and the area of occupancy (AOO) as 20 km², based on a cell width of 2 km as recommended by the IUCN Standards and Petitions Committee (2024). Due to its limited geographical range (AOO <500 km²), with only five known localities and habitat under pressure from prolonged drought conditions, *Petalidium saxatile* is here provisionally assessed as Endangered EN B2a,b(iii) (IUCN 2012).

Etymology:—The specific epithet refers to the habitat in which *Petalidium saxatile* is most often found; derived from the Latin ‘*saxatilis*’, dwelling or found among rocks (Stearn 2004).

Notes:—*Petalidium saxatile* is morphologically most similar to *P. canescens* and *P. setosum*. Hence these three species were compared in the diagnosis above. Some of the morphological features to distinguish between *P. canescens*, *P. saxatile*, and *P. setosum* are provided in Table 1; also see Figs 4 & 5.

TABLE 1. Prominent morphological differences among *Petalidium saxatile*, *P. canescens*, and *P. setosum*.

Character	<i>P. saxatile</i>	<i>P. canescens</i>	<i>P. setosum</i>
Indumentum on vegetative parts	Simple, bifurcate, stellate-dendritic, dendritic and stalked glandular trichomes, in addition also long, robust, simple trichomes	Strigose, on stems and petioles widely spaced long, robust, simple multi-cellular trichomes in addition, rarely also on leaf margins	Simple and stalked glandular trichomes and sessile glands, in addition also long, robust, simple multi-cellular ones
Leaves (shape)	Narrowly ovate, lanceolate (Lindley) or elliptic; conduplicate	Broadly ovate or narrowly to broadly lanceolate (Lindley); flat or sub-conduplicate	Broadly to narrowly ovate, lanceolate, lanceolate (Lindley) or elliptic; surface variable: flat, irregularly curved, twisted, widely undulate, recurved or incurved towards margins
Leaves (lamina size) (mm)	13–70 × 4–22	Broad-leaved form: 10–90 × 9–100 Narrow-leaved form: 6–90 × 2–30	18–74 × 7–50
Leaves (length vs. width ratio)	3.0–3.3: 1	Broad-leaved form: 0.9–1.4: 1 Narrow-leaved form: 3.0–3.5: 1	1.5–3.3: 1
Bracteoles (indumentum (abaxially))	Similar to vegetative parts but lacking bifurcate, stellate-dendritic and dendritic trichomes	Sparsely strigose, sometimes towards apex only, often in addition few robust, simple, multicellular eglandular trichomes towards apex	Similar to vegetative parts but denser
Calyx (indumentum)	Strigose both sides	Strigose both sides, sparsely abaxially	Strigose both sides with small, short-stalked glandular trichomes in addition abaxially
Corolla (length) (mm) (lobes straightened)	23.3–26.3	23.2–32.0	19.4–20.2
Corolla tube expanded portion (length) (mm)	7.7–9.1	ca. 7.5	ca. 3.4
Corolla upper lobes (shape; fusion)	Tapering or ovate, apices rounded; connate for 35–40% of their length	Obovate, apices retuse; connate for 24% of their length	Obovate or rectangular, apices retuse or truncate; connate for 35% of their length
Corolla lateral lobes (shape)	Tapering or ovate, apices rounded	Rectangular, apices retuse	Rectangular, apices retuse or truncate
Corolla anterior lobe (shape)	Tapering, obovate or rectangular, apex retuse	Obovate, apex retuse	Obovate, apex retuse or truncate, ca. 6.3 × 4.8

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TABLE 1. (Continued)

Character	<i>P. saxatile</i>	<i>P. canescens</i>	<i>P. setosum</i>
Corolla lobes (colour, adaxially)	Anterior lobe bright yellow, lateral and upper lobes pink or brown-pink, darker towards bases; traces conspicuous	All lobes similarly coloured violet-red but anterior lobe darker; traces conspicuous	All lobes similarly coloured: purple, burgundy or carmine or anterior lobe as above but yellow towards apex; traces inconspicuous
Corolla nectar guides (anterior lobe)	Absent	Dark red or inconspicuous	Yellow, conspicuous
Style (indumentum)	Puberulous	Puberulous	Puberulous with scattered small, short-stalked glandular trichomes in addition
Ovary (indumentum)	Glabrous	Glabrous	Scattered small, stalked glandular trichomes towards apex, otherwise glabrous
Distribution	Kunene Region in vicinity of Palmwag and southwards to the Bergsig area, with an outlier population near Khorixas, Northwestern Namibia	Kunene Region from Khorixas district southwards to Erongo Region Swakopund District and eastwards to Otjozondjupa Region Okahandja District	Kunene Region in vicinity of Sorris, southwards to Erongo Region, western Khomas and Hardap Regions to the southern Kharas Region, Namibia. Also in South Africa (Northern Cape Province)

In the case of herbarium specimens, the new species may be mistaken not only for *P. canescens* and *P. setosum*, but also for other *Petalidium* species from Namibia's Kunene Region that have compact inflorescences and indumentum consisting of dendritic trichomes. Notably, these include *P. halimoides* Moore (1880: 228) and *P. lanatum* Clarke (1899: 90). However, *Petalidium halimoides* and *P. lanatum* have relatively small corollas, 12–13 mm long (*vs.* ca. double the length, 23–26 mm) and the indumentum on the bracts lacks long, simple trichomes (*vs.* long simple trichomes present, visible to the naked eye). All the mentioned taxa are from the group composed of plants with irregular, four-parted calyces (Obermeijer 1936, Tripp *et al.* 2017).

Our phylogenetic analyses show that *P. saxatile* is genetically distinct from *P. canescens* and other species of *Petalidium* found nearby, forming a reciprocally monophyletic clade in our phylogenetic analysis (Fig. 6A). Further, a network analysis that aimed to assess a history of hybridisation or incomplete lineage sorting in *P. saxatile* and close relatives shows that *P. saxatile* clearly forms a cohesive genetic cluster that is distinct from other species (Fig. 6B). We take these results as supportive of the idea that *P. saxatile* is a 'good species' with respect to the general lineage concept of species (De Quieroz 1998), although further phylogenetic investigations that include *P. setosum* would be useful to confirm this.

The Etendeka Tableland, a prominent dissected plateau in arid northwestern Namibia, aligns closely with the core distribution area of *P. saxatile* (Detay & Detay 2017, Atlas of Namibia Team 2022). This landscape formed around 132 million years ago due to volcanic activity, specifically lava flows from the Etendeka Group basalts, associated with the initial seafloor spreading that eventually created the South Atlantic Ocean (Goudie & Viles 2015). Although the region is known to be floristically diverse, no comprehensive plant checklist has yet been compiled. A limited ecological study of several mesas (flat-topped, isolated hills) in the area recorded 331 plant species, representing over 7% of Namibia's known plant species, despite the study covering only 0.1% of the country's land area (Burke 2003). Recently, we described *P. etendekaense* Swanepoel, E.A.Tripp & A.E.van Wyk in Swanepoel *et al.* (2024: 37), a species exclusive to the Etendeka Tableland. Known populations of *P. etendekaense* and *P. saxatile* do not overlap, thus showing allopatric distributions. Other *Petalidium* species endemic or near-endemic to the Etendeka Tableland include *P. giessii*, *P. luteoalbum*, and *P. ovatum* (Schinz 1890: 198) Clarke (1899: 90). Another notable endemic species from this region is *Oberholzeria etendekaensis* Swanepoel, M.M.le Roux, M.F.Wojc. & A.E.van Wyk in Swanepoel *et al.* (2015: 11) (Fabaceae), a succulent biennial or short-lived perennial shrublet that belongs to a monotypic genus. This suggests the Etendeka Tableland may serve as a local subcentre of plant endemism within the larger Kaokoveld Centre of Endemism, a topic that merits further research.



FIGURE 4. *Petalidium canescens*, morphology of leaves and flowers. **A.** Plant of broad-leaved form, with inflorescences borne mainly just above ground-level. **B.** Plant of narrow-leaved form. **C.** Flower in front view; all lobes similarly coloured violet-red, but anterior lobe darker; traces conspicuous. **D.** Flower in oblique-lateral view. **E.** Inflorescences with flowers. Photographs by W. Swanepoel.



FIGURE 5. *Petalidium setosum*, morphology of leaves and flowers. **A.** Plant with old persistent inflorescences; note relatively flat or irregularly twisted leaf blades. **B.** Shoot showing relatively broad leaves with the blade not conspicuously folded upwards along the midrib, and with greyish indumentum. **C, D, E, F.** Flowers in front view, each image from a different plant to show variation in colour; note all corolla lobes of a flower being similarly coloured, or anterior lobe inside (adaxially) same colour as the other lobes but yellow towards apex (**C, F**). Anterior corolla lobe always with yellow nectar guides. Photographs by W. Swanepoel.

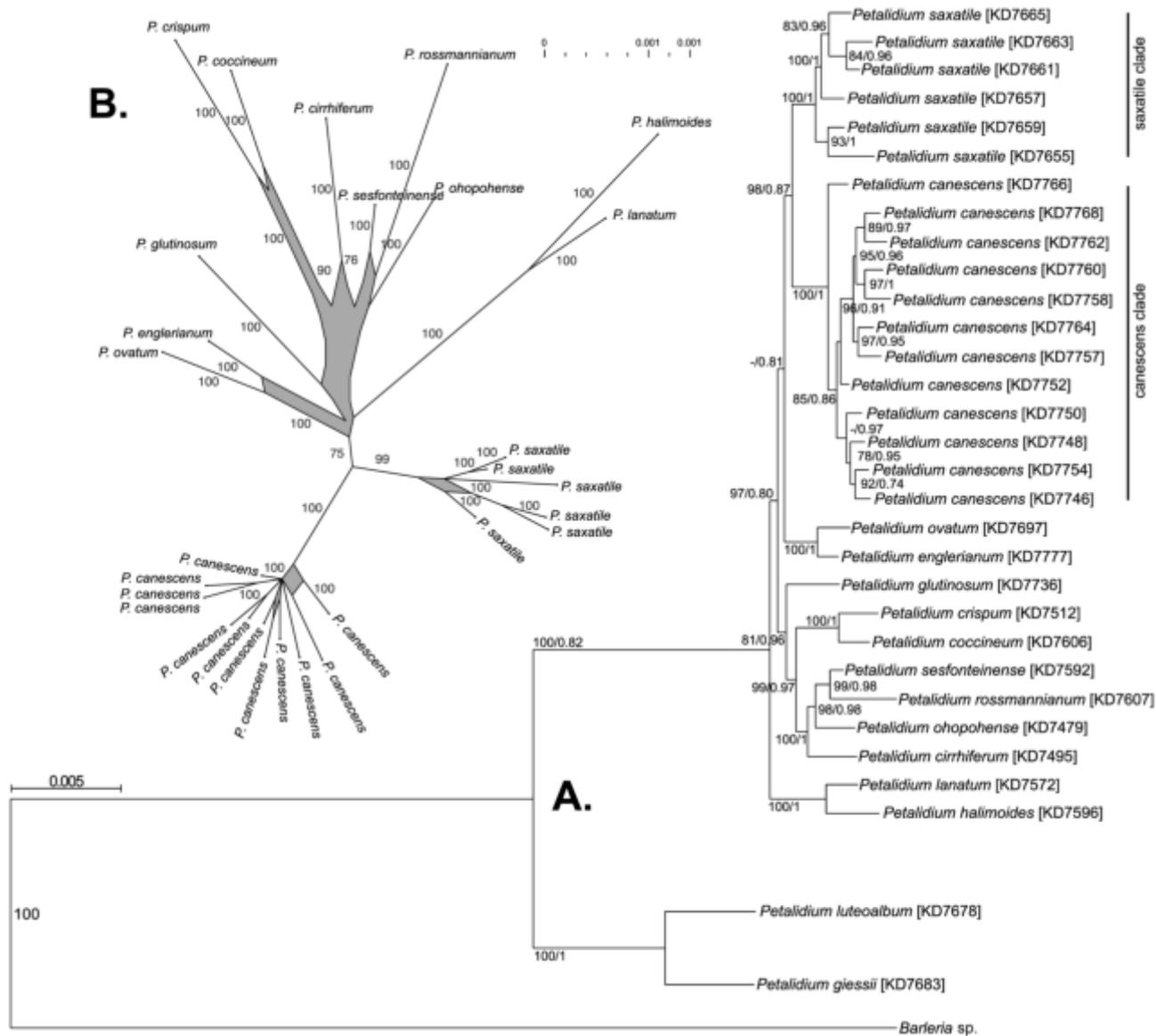


FIGURE 6. Genetic distinctness of *Petalidium saxatile*. **A.** Maximum likelihood phylogenetic tree for *P. saxatile*, *P. canescens*, and other species of *Petalidium* that occur in the region (the topology from Bayesian analyses was identical). Branch support is given when higher than 75% of bootstrap replicates in maximum likelihood analysis and higher than 0.80 in the Bayesian analysis. At each tip, the species names is followed by the sample name as submitted to SRA-NCBI database (in brackets). **B.** A neighbour network that checks for reticulated evolutionary events between clusters that do not form a clear hierarchy. Reticulations are here represented as grey areas. The statistical support for the main nodes are given (in terms of percentage of bootstrap replicates that have that relationship).

Additional specimens examined (paratypes):—NAMIBIA, Kunene Region: On plain in Aub River valley, 1913DD, 1120 m, 4 June 2000, *Gindrig & Hennig 104* (PRE!, WIND!); 4.7 km from Palmwag on road C43 to Sesfontein, 1913DD, 901 m, 4 May 2022, *Dexter & Loiseau 7655* (E!, LUBA!, WIND!); 4.7 km from Palmwag on road C43 to Sesfontein, 1913DD, 901 m, 11 May 2022, *Swanepoel 646* (WIND!); Achab River, 2013BB, 6 June 1999, *Hearn 28* (WIND!); Farm Welbedacht 394, 2014DB, May 1949, *Liebenberg 4954* (PRE, WIND!).

The outlier locality mentioned on the label of the specimen *Liebenberg 4954* (WIND), cited above, may be incorrect. A duplicate of this collection in Herb. PRE provides the same locality, but also includes the name “Fransfontein,” a village located just north of Khorixas. We interpret this additional information as likely intended to help identify the location of the farm Welbedacht. During a visit in November 2024 to the farm Welbedacht 394, south of Khorixas, one of us (WS) found no outcrops of Etendeka Group rocks, which serve as the substrate at all other known sites of *P. saxatile*. Furthermore, an extensive search of the farm for *Petalidium* species revealed no trace of *P. saxatile*, but only the presence of *P. halimoides*.

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