Monograph on

Endemism in the Highlands and Escarpments of Angola and Namibia

Angola Cave-Chat *Xenocopsychus ansorgei*
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Editors:

John M Mendelsohn
Brian J Huntley
Pedro Vaz Pinto

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Diversity and endemism

High endemism of the genus *Petalidium* (Acanthaceae) in the highlands and escarpments of Angola and Namibia

KG Dexter[1,2], W Swanepoel[3,4], O Loiseau[1], I Darbyshire[5], L Nanyeni[6], FM Gonçalves[7,8], F Chase[9], EA Manzitto-Tripp[10]

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[1] School of GeoSciences, University of Edinburgh, Edinburgh, UK; kyle.dexter@ed.ac.uk
[2] Royal Botanic Garden Edinburgh, Edinburgh, UK
[3] Independent Researcher, PO Box 21168, Windhoek, Namibia
[4] HGWJ Schweickerdt Herbarium, University of Pretoria, Pretoria, South Africa
[5] Royal Botanic Gardens Kew, Richmond, Surrey, UK
[6] National Botanical Research Institute, Windhoek, Namibia
[7] Instituto Superior de Ciências de Educação, Huíla, Angola
[8] Universidade Mandume Ya Ndemufayo, Lubango, Angola
[9] Namibia Nature Foundation, Windhoek, Namibia
[10] University of Colorado – Boulder, Colorado, USA

ABSTRACT
Petalidium (Acanthaceae) is a speciose genus of woody shrubs with its diversity centred in arid regions of central to northwestern Namibia and southwestern Angola. Here, we compiled distribution information for all accepted species in the genus from herbarium specimens and our own fieldwork to determine the number of endemics and near-endemic species in the highlands and escarpments of Angola and Namibia (HEAN). In the process, we provide an informal overview of all accepted species of *Petalidium*, which we hope will facilitate further research on the genus. We found that 22 of 36 species are endemic or near-endemic to the HEAN, clearly indicating the importance of this area for plant conservation. Furthermore, our results presented here, coupled with evolutionary studies that show the genus to be rapidly diversifying, suggest that the highlands and escarpments have played a significant role in plant speciation. We conclude by highlighting the advantages of studying this genus further as a model system for plant ecology and evolution in arid environments.

Keywords: Angola, deserts, endemism, escarpments, highlands, Namibia, *Petalidium*

A BRIEF INTRODUCTION TO *PETALIDIUM*

Petalidium Nees (Acanthaceae) is one of the iconic plant genera of arid regions of central and northwestern Namibia and southwestern Angola. It is the third-most diverse plant genus in the Kaokoveld Centre of Endemism, which lies at the core of the Highlands and Escarpments of Angola and Namibia (HEAN), after *Euphorbia* L. (Euphorbiaceae) and *Indigofera* L. (Fabaceae) (Craven 2009). It also has several species in the Gariep Centre of Endemism, although these species are not particularly associated with the HEAN (van Wyk & Smith 2001). *Petalidium* is one of four evolutionary radiations of Acanthaceae in western Namibia and southwestern Angola, the others being *Monechma* Hochst., *Blepharis* Juss. and *Barleria* L. (Fisher *et al.* 2015, Tripp *et al.* 2017, Darbyshire *et al.* 2020). These other genera, both within and outside of Acanthaceae, are widespread and diverse beyond the HEAN, while most species of *Petalidium* are restricted to the HEAN and neighbouring areas in Namibia and Angola. As a monophyletic radiation in and around the HEAN (Loiseau *et al.* 2023), *Petalidium* represents an ideal system for understanding the biodiversity patterns and evolutionary history of this study area.

Petalidium is not a montane genus per se; many of its species occupy areas of lower elevation within the HEAN and other species occur in flatter areas towards the Atlantic Ocean or in non-montane areas east of the HEAN (Figure 1). Nevertheless, it seems probable that the rugged topography of the HEAN has played a significant role in the diversification of *Petalidium* (Tripp *et al*. 2017, Loiseau *et al.* 2023). Many species of *Petalidium* are characterised by having small populations, and mountain barriers may have contributed to allopatric isolation (Hughes & Atchison 2015). Complex topography also interposes diverse geological and edaphic substrates which can drive plant speciation (Kruckeberg 1986).

Petalidium varies in its growth form from entirely prostrate plants in hyperarid areas, namely the Namib Desert, to upright shrubs that can reach 2 m in height (e.g., *P. bracteatum* and *P.* sp. nov. Dexter & Tripp 7296). Plants of *Petalidium* always have at least some aboveground woody tissue and often bear taproots which can exceed 80 cm in length. *Petalidium* is distinguished from other Acanthaceae in the region by its paired, leaflike bracts, two-seeded capsules with fracturing placentae, triangular pollen in polar view with 12 pseudocolpi, and four areas of raised

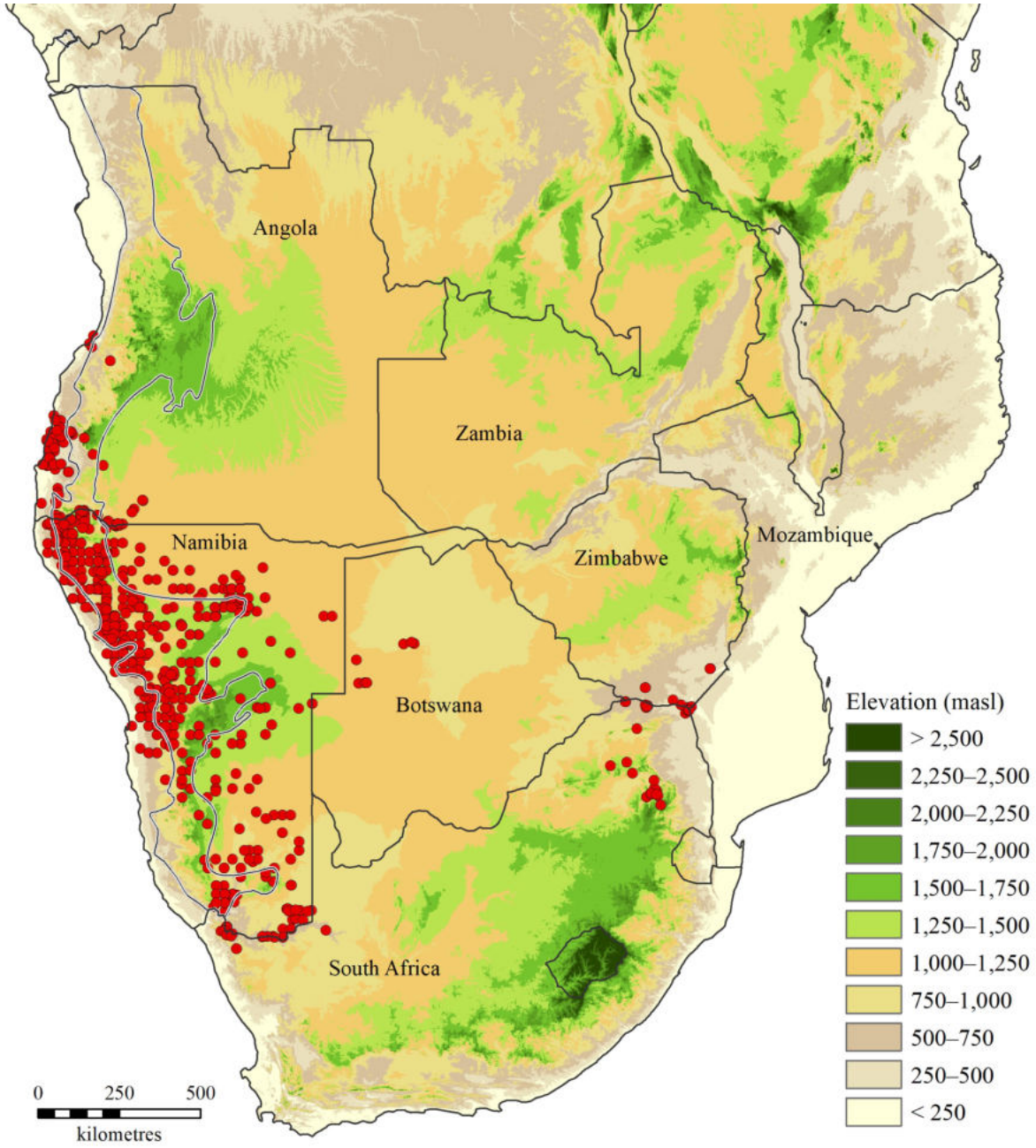

Figure 1: *Occurrences of* Petalidium *across southern Africa. Each red dot represents a georeferenced herbarium voucher, with data derived from vouchers primarily held at the Natural History Museum Herbarium (BM), University of Colorado Museum Herbarium (COLO), Royal Botanic Garden Edinburgh Herbarium (E), Royal Botanic Gardens Herbarium (K), Instituto Superior de Ciencias da Educação Herbarium (LUBA), South African National Biodiversity Institute National Herbarium (PRE) and the National Herbarium of Namibia (WIND). The background colour of the map depicts the elevation in metres above sea level. The grey lines represent country borders, while the black line with white shadowing shows the limits of the highlands and escarpments of Angola and Namibia.*

tectum on the pollen surrounding each aperture (Tripp *et al.* 2013, Manzitto-Tripp *et al.* 2021). Like some other genera of Acanthaceae (e.g., *Ruellia*; Tripp *et al.* 2021), *Petalidium* displays a remarkable diversity of floral forms, varying from large campanulate, open flowers to tubular red flowers that attract sunbirds and minute maroon flowers that are probably pollinated by long-tongued flies.

In this contribution, we give an overview of our current understanding of the genus, including a brief description of all known species. We present distribution maps for each species based on our own fieldwork and reviews of herbarium vouchers at the herbaria that house most existing specimens of *Petalidium* worldwide (BM, K, LUBA, PRE and WIND). There has been no taxonomic revision of *Petalidium* since Obermeyer (1936), and that work

only included 18 species. Our contribution here represents the combined and current knowledge of several scientists that are actively working on the genus. Future systematic and taxonomic research may very well change our understanding of the morphological limits of individual species and their geographical distributions, but our contribution here represents the most up-to-date information available. Overall, we find that nearly two thirds (22 of 36) of the accepted African species of *Petalidium* represent endemics or near-endemics of the HEAN.

INFORMAL MORPHOLOGICAL GROUPS, THEIR CONSTITUENT SPECIES AND GEOGRAPHICAL DISTRIBUTIONS

The following five groups used to categorise species of *Petalidium* are based largely on the morphology of the overall inflorescence and individual flowers. In some cases, the groups appear to be 'natural', or reciprocally monophyletic, in the latest phylogenies produced for *Petalidium*. In other cases, the groups are clearly not monophyletic. Our phylogenetic understanding of the relationships of species of *Petalidium* is a work in progress, and we only give reference to the phylogenetic nature of groups where we are confident in that result based on our phylogenetic studies to date (Tripp *et al.* 2017, Loiseau *et al.* 2023).

1. Large-, open-flowered group

This group consists of ten species known to date that are characterised by their large, open campanulate flowers. The androecium and gynoecium are bilaterally symmetric, like all species in the genus, but the corolla approaches radial symmetry. Hereafter, when we refer to floral symmetry, we are referring to the form of the corolla. The species in this group represent the earliest diverging branches in the phylogeny of *Petalidium* (Loiseau *et al.* 2023), and their floral form may represent the ancestral form for the genus. The colour of the flowers varies from white to yellow to light pink and purple. The species in this group are mostly upright shrubs and tend to occur in cooler, moister areas with less water stress than most other species of *Petalidium* that occur in the HEAN and the Namib Desert.

HEAN endemics

Petalidium cymbiforme Schinz: This species (Figure 2) is distinguished from other species in this group by its combination of narrow, linear leaves and white flowers. It is restricted to the southernmost portion of the HEAN. Note that for Figures 2–36 the colours and lines shown in the distribution maps are the same as those described in Figure 1.

Petalidium luteo-album A.Meeuse: This species (Figure 3) and *P. giessii* (Figure 4) are close relatives that occur in hyperarid areas, in contrast to the other species in the group. They are similar in having large papery cordate bracts that are persistent long after the flowers fall. They can be distinguished from each other by their flower colour, with *P. luteo-album* having mostly cream to white corolla lobes (except for the lower corolla lobe, which is yellow), while *P. giessii* has all corolla lobes yellow. The bracts of *P. luteo-album* are larger, more opaque, often drying red or brown, and more strongly cordate. *Petalidium*

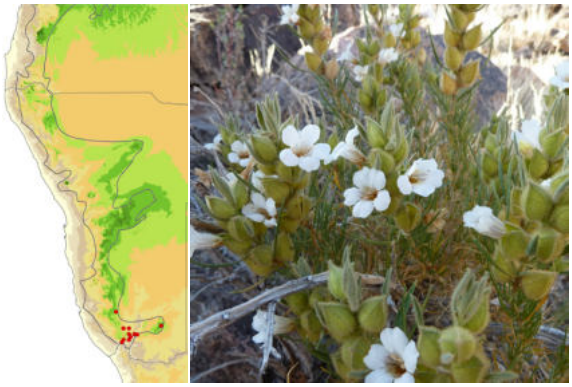

Figure 2: *Occurrences of* Petalidium cymbiforme *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 2078.*

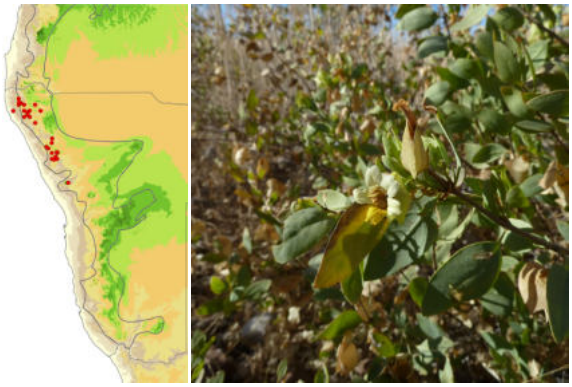

Figure 3: *Occurrences of* Petalidium luteo-album *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 830.*

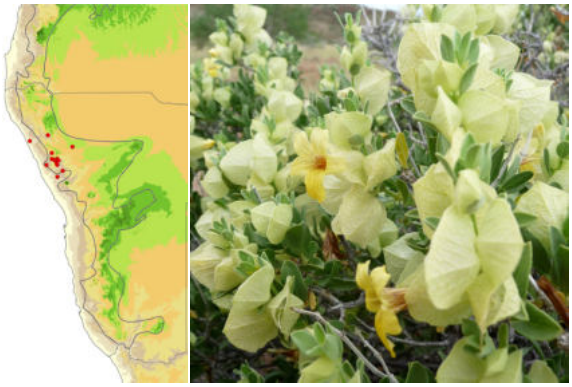

Figure 4: *Occurrences of* Petalidium giessii *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 825.*

luteo-album also has a larger range yet is more clearly restricted to the HEAN than *P. giesii*.

HEAN near-endemics

Petalidium giessii P.G.Mey.: See *P. luteo-album* (above) for morphological differences with that species. *Petalidium giessii* occurs in the HEAN, but also at lower elevations to the west of the escarpment on the Namibian coastal plain (Figure 4).

Petalidium rautanenii Schinz: This is the only species from the 'large, open-flowered group' that occurs in central northern Namibia. It is found at the northeastern extreme of the highlands in Namibia around the Otavi Mountains, but also occurs in surrounding areas just outside the designated highland area (Figure 5).

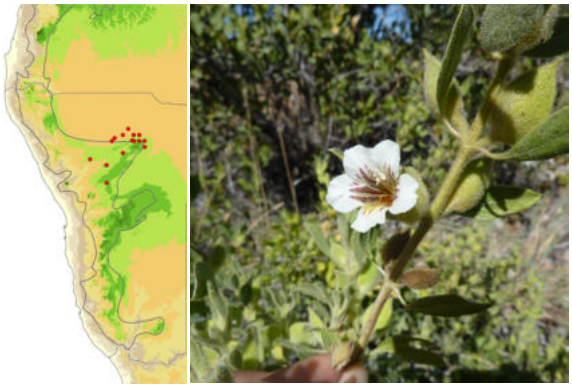

Figure 5: *Occurrences of* Petalidium rautanenii *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 4796.*

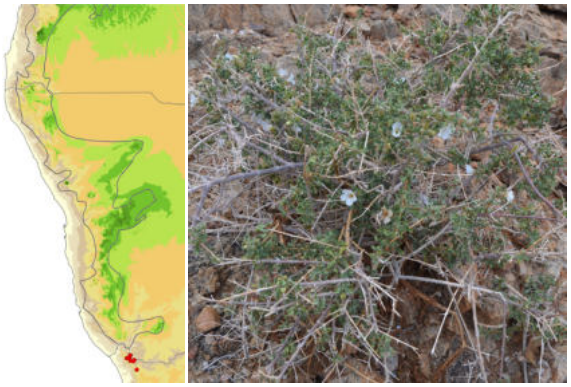

Figure 8: *Occurrences of* Petalidium mannheimerae *with photograph (by L Nanyeni) of individual vouchered as Nanyeni 936.*

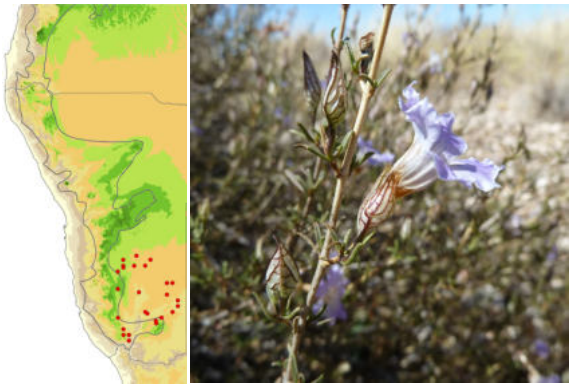

Figure 6: *Occurrences of* Petalidium linifolium *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 2031.*

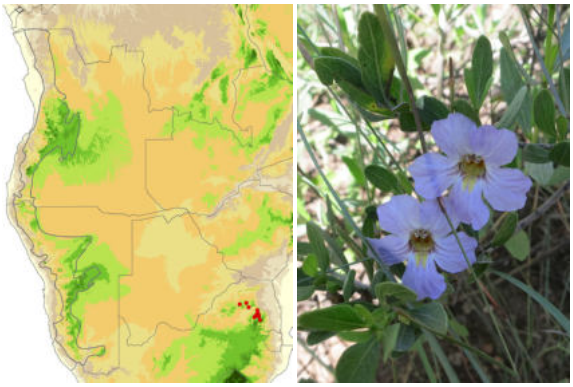

Figure 9: *Occurrences of* Petalidium oblongifolium *with photograph (by K Dexter) of individual vouchered as Dexter 6859.*

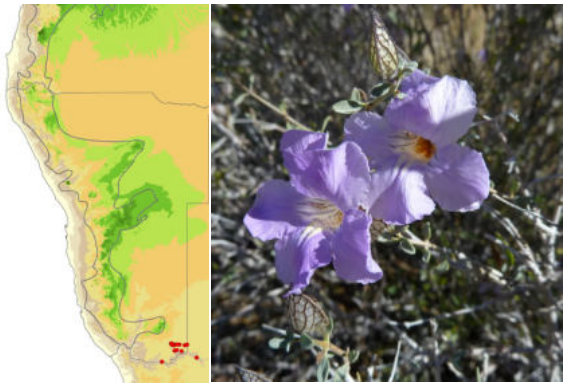

Figure 7: *Occurrences of* Petalidium lucens *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 2065.*

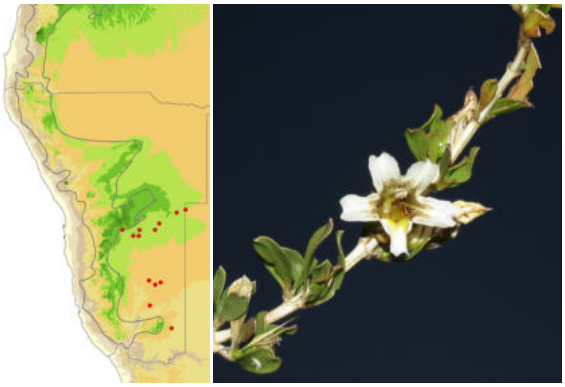

Figure 10: *Occurrences of* Petalidium parvifolium *with photograph (by W Swanepoel) of individual vouchered as Swanepoel 623.*

Other species not associated with the highlands and escarpment

Petalidium barlerioides (B.Heyne ex Roth) Nees: This is the only species of *Petalidium* whose range is outside of Africa, and it is the sister species to the rest of the genus (Tripp *et al.* 2017). It occurs in the Himalayan foothills of India and Nepal, and elsewhere in India. No map or photo shown.

Petalidium linifolium T.Anderson: This species is similar to *P. cymbiforme* (above) in its linear leaves, but has pale pink to purple flowers. It does occur in the southern portion of the HEAN, but also further eastward and does not seem particularly associated with the HEAN (Figure 6).

Petalidium lucens Oberm.: This species (Figure 7) is easily confused with *P. parvifolium* (Figure 10), and questions persist about distinctions among the two. However, they appear to be geographically segregated, with *P. lucens* occurring along the most southerly border of Namibia with South Africa. This species occurs well eastward of the HEAN.

Petalidium mannheimerae Swanepoel, Nanyeni & A.E.van Wyk: Illustrated in Figure 8, this is a recently described species that was previously lumped with *P. parvifolium* (Figure 10) and is also similar to *P. lucens* (Figure 7). It is distinguished from these species in its uniformly white flowers, semi-succulent leaves and puberulent indumentum on vegetative parts. It occurs just to the south of the southern end of the HEAN (Figure 8).

Petalidium oblongifolium C.B.Clarke: This is the earliest diverging species among African *Petalidium* and is geographically segregated from the remainder, occurring in the Mpumalanga and Limpopo provinces of South Africa (Figure 9). It occupies more mesic environments than all other African species in the genus.

Petalidium parvifolium Schinz: As with *P. lucens* (Figure 7), this species (Figure 10) has large purple to pink to white flowers, elliptic to lanceolate (rather than linear) leaves and papery, semi-transparent bracts with marked venation. It is found east of the highlands and escarpment of central and southern Namibia, as far north as Rehoboth and Gobabis, and is also found in central-western Botswana.

2. Midsized-, open-flowered group

This group of species has smaller flowers than the previous group, but with a similar overall form, approaching radial symmetry, albeit perhaps more clearly bilateral. The colour of the flowers varies from white to yellow to light or deep pink, purple and even magenta, sometimes within individual species. Many species in this group show high variability in growth form, from upright shrubs in areas with higher water availability to completely prostrate forms in the Namib Desert. Most species in this group are associated with the highlands and escarpments of Namibia and southern Angola.

HEAN endemics

Petalidium ohopohense P.G.Mey.: This species is distinguished from others in the group by its consistently prostrate growth form and flowers that have larger corolla lobes that are consistently pink. It is restricted to a small area around the town of Opuwo (Figure 11).

Petalidium rossmanianum P.G.Mey.: This species has a relatively large range across the northern highlands and escarpment within Namibia (Figure 12). Its flowers vary from white (with coloured nectar guides) to pink to purple and is superficially easy to confuse with *P. variabile* (Figure 17). They are distinguished in their pubescence (branching in *P. rossmanianum*, not so in *P. variabile*), and their ranges do not overlap.

Petalidium sesfonteinense Swanepoel & E.Tripp: This species (Figure 13) is similar to *P. rossmanianum* (Figure 12) and *P. variabile* (Figure 17), but is

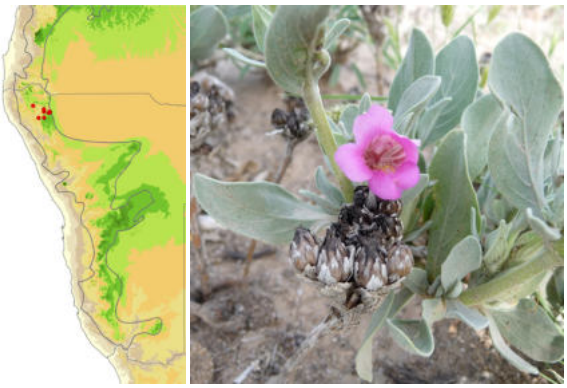

Figure 11: *Occurrences of* Petalidium ohopohense *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 849.*

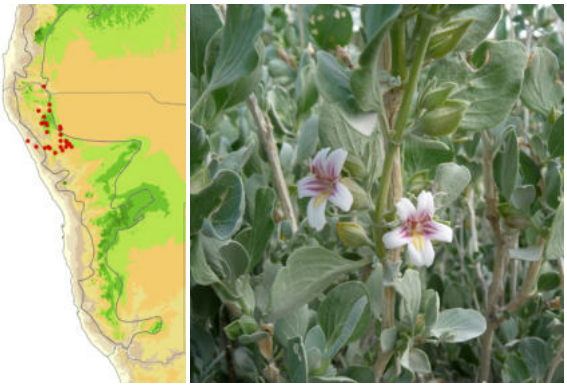

Figure 12: *Occurrences of* Petalidium rossmanianum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 832.*

distinguished by dense dentritic and glandular trichomes. The trichomes of *P. rossmanianum* are not as dense as *P. sesfonteinense* and are not generally glandular. *Petalidium sesfonteinense* shows high variability in flower colour like *P. rossmanianum* and *P. variabile*. It is restricted to a relatively small area around Sesfontein in Namibia and westwards.

Petalidium subcrispum P.G.Mey.: This species (Figure 14) is vegetatively distinct from all other species in this group, having densely pubescent and pungent leaves with an undulate margin. In fact, vegetatively it is very similar to *P. crispum* (Figure 23) including vegetative odours nearly indistinguishable to the human nose, but the flowers are completely different (open cup-shaped flowers in *P. subcrispum* versus tubular orange flowers in *P. crispum*). This species has a very narrow range in the northern Kaokoveld of Namibia.

HEAN near-endemics

Petalidium canescens (Engl.) C.B.Clarke: Of the species with the characteristic flowers of this group, this is the only one where the inflorescence consists of a clustered 'head' (Figure 15), which in this case is sub-woody, similar to *P. setosum* (Figure 34). The individual flowers project from this congested head-like structure. Individuals of *P. canescens* can be quite small even when flowering (10 cm x 10 cm), but they do still bear aboveground woody tissue. This species occupies the central highlands and escarpment of Namibia and occurs peripherally into the Namibian coastal plain.

Petalidium pilosi-bracteolatum Merxm. & Hainz: This species (Figure 16) is most easily confused with *P. rossmanianum* (Figure 12) and *P. variabile* (Figure 17), but its flowers are more consistently dark pink and the bracts subtending the flowers typically bear long, straight, glandular trichomes. The species appears to have two disjunct areas of distribution, a northern one restricted to the HEAN and centred around Bergsig and a southern one that occurs in the HEAN and also on the coastal plain towards Swakopmund.

Petalidium variabile (Engl.) C.B.Clarke: This species (Figure 17) resembles many others in the group and is rather variable, as the specific epithet indicates, but is consistently distinguished from others by its unbranched trichomes. Similar to *P. canescens* (Figure 15), it occurs across the central highlands and escarpment of Namibia, and extends into the Namibian coastal plain.

Figure 13: *Occurrences of* Petalidium sesfonteinense *with photograph (by K Dexter) of individual vouchered as Dexter 7559.*

Figure 14: *Occurrences of* Petalidium subcrispum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 2013.*

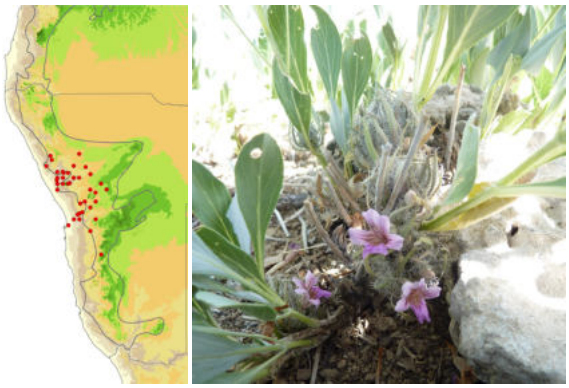

Figure 15: *Occurrences of* Petalidium canescens *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 882.*

Figure 16: *Occurrences of* Petalidium pilosi-bracteolatum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 4096.*

Petalidium welwitschii S.Moore: This species has long pubescence across the leaves and inflorescence, often glandular, which sets it apart from other species in the group. It is also the most northerly distributed, being common in southwest Angola (Figure 18). Within Angola, it regularly occurs on the coastal plain, but is otherwise mostly restricted to the highlands and escarpments in Namibia.

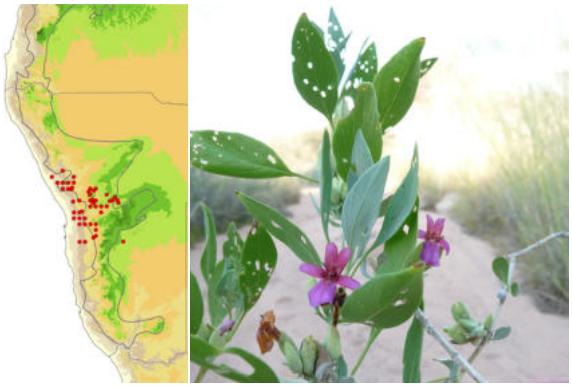

Figure 17: *Occurrences of* Petalidium variabile *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 776.*

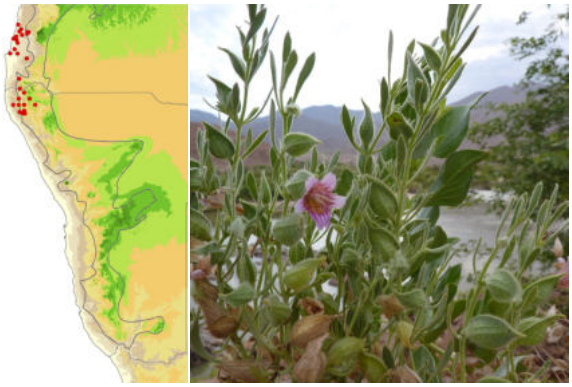

Figure 18: *Occurrences of* Petalidium welwitschii *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 4085.*

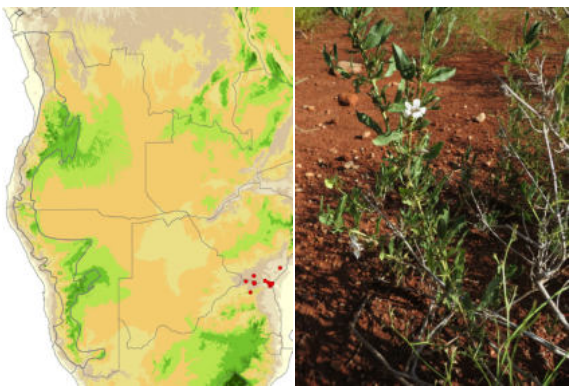

Figure 19: *Occurrences of* Petalidium aromaticum *with photograph (by K Dexter) of individual vouchered as Dexter 6862.*

Other species not associated with the HEAN

Petalidium aromaticum Oberm.: This species consistently bears white flowers, in contrast to most other species in the group. It occurs in the Limpopo Province of South Africa and across the border into Zimbabwe, well disjunct from all other species of *Petalidium* (Figure 19).

Petalidium englerianum (Schinz) C.B.Clarke: This species is distinguished from others in the uniformly glaucous appearance of the vegetation (Figure 20). In other species, some leaves on an individual may appear glaucous, but other leaves on the same individual are green. It is also distinct in having orange to brown upper petals with a yellow lower petal. It occurs in the central highlands of Namibia, but also well eastward across Kalahari sands into Botswana. There is one set of populations at the western edge of its range that has flowers resembling *P. physaloides* (Figure 31; maroon and with a more bilaterally symmetric coralla), and this may represent a novel species endemic to the HEAN.

Petalidium rupestre S.Moore: This species has white flowers but is perhaps most distinct in its incredibly sticky leaves that are flabellate to nearly reniform in shape. The species has a very narrow distribution

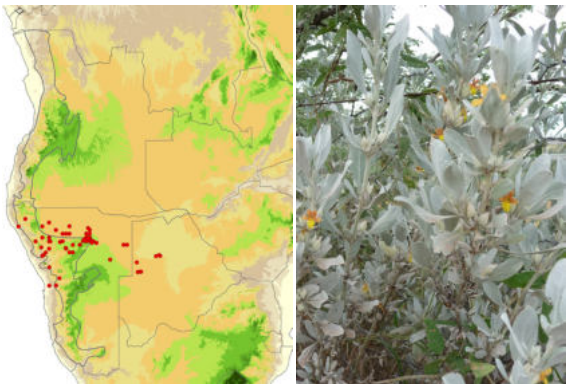

Figure 20: *Occurrences of* Petalidium englerianum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 778.*

Figure 21: *Occurrences of* Petalidium rupestre *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 6964.*

along the rocky walls of the gorge of the Rio Giraul, set in the coastal plain of Angola (Figure 21).

3. Long, tubular-flowered group

All the species in this group have tubular flowers that are strongly exerted from between the two bracts. The flower colour varies from orange to red to dark pinkish purple to white. Most of these species have a floral morphology that suggests sunbird pollination, while the white flowers of *P. angustitubum* (Figure 25) rather suggest pollination by sphingid moths or other nocturnal animals.

HEAN endemics

Petalidium coccineum S.Moore: This species (Figure 22) is similar to *P. crispum* (Figure 23) in its orange to red, curving tubular inflorescence, but tends to occur in sandy washes rather than on rocky slopes. It forms a more upright shrub than *P. crispum*, albeit still with an overall sprawling growth form. Amongst the species in the group, this species has the widest distribution, ranging from across northwest Namibia into southwest Angola. Locally, however, it is typically rare, occurring as one to a few scattered individuals.

Petalidium crispum A.Meeuse ex P.G.Mey.: This species (Figure 23) is similar to *P. coccineum*, but is distinguished on several characters outlined above, additionally by its stickier leaves with an undulate margin (see also *P. subcrispum*, Figure 14). It has a fairly narrow distribution within the far northwestern highlands of Namibia.

Petalidium huillense C.B.Clarke: This species has axillary spines (Figure 24), which is unique in the genus. (Note: we consider *P. spiniferum* to be a synonym of this species.) We have limited observations of the floral morphology on living individuals, while herbarium specimens suggest partially exerted flowers, verging on tubular, which are most similar to those of *P. glandulosum* (Figure 27). *Petalidium huillense* has a restricted distribution along and near the Cunene River as it traverses the HEAN.

HEAN near-endemics

Petalidium angustitubum P.G.Mey.: This is the only species in the genus with white tubular flowers (Figure 25). It has a narrow geographic range on the western edge of the escarpment in northern Namibia, with scattered peripheral populations into the coastal plain.

Other species not associated with the HEAN

Petalidium bracteatum Oberm.: This species (Figure 26) resembles *P. coccineum* (Figure 22) but is a taller plant overall, sometimes scandent on other shrubs or rocks, and the flowers are larger and deeper red in colour (rather than orange). It occurs primarily east

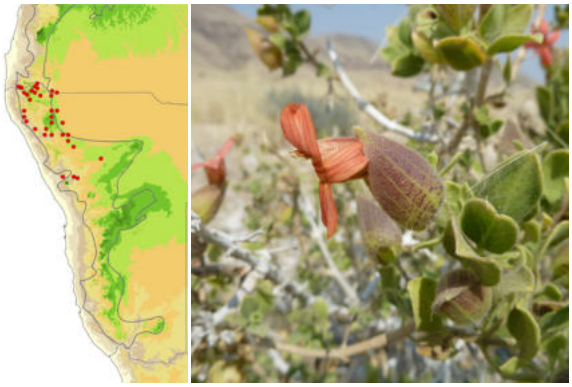

Figure 22: *Occurrences of* Petalidium coccineum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 872.*

Figure 23: *Occurrences of* Petalidium crispum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 4056.*

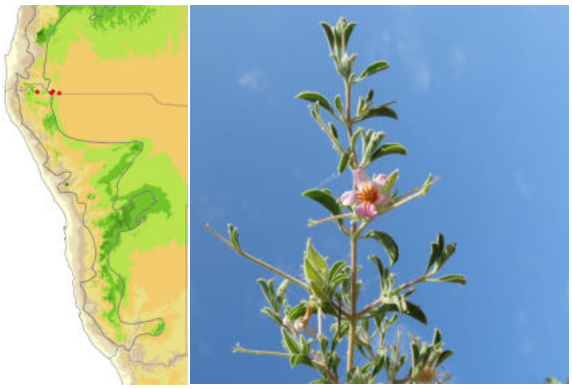

Figure 24: *Occurrences of* Petalidium huillense *with photograph (by W Swanepoel) of individual vouchered as Swanepoel 631.*

of the highlands in northern Namibia and southern Angola; most records from the HEAN are likely to represent misidentifications of *P. coccineum*.

Petalidium glandulosum S.Moore: This species has flowers that are less orange or red than others in the group, tending towards dark pink to purple (Figure 27). The flowers have a characteristic bend in the tubular part of the flower. The species is primarily distributed on the coastal plain of Angola, with an

outlying northern population near Benguela that may represent a new species and certainly the most northerly population of *Petalidium* in Africa.

4. Midsized-, maroon-flowered group

This group of species has a flower type that can be considered intermediate in form between the group with minute maroon flowers (see below) and that with long tubular flowers (see above). The flowers of this fourth group often have the colouration of the minute-, maroon-flowered group, yet they are larger in size. In colour, the flowers are darker than any in the previous groups, being either maroon or deep purple to pink. The species in the group often have a thick base to the trunk, sometimes over 10 cm in diameter, and can form large upright shrubs.

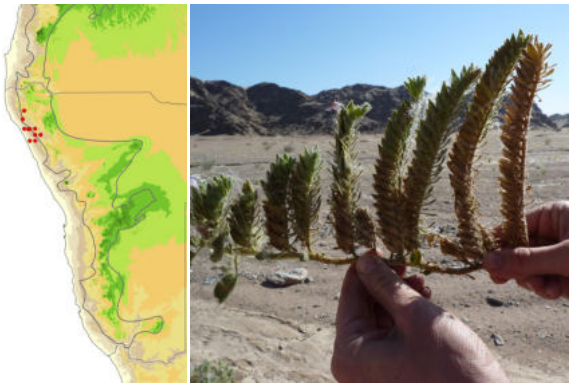

Figure 25: *Occurrences of* Petalidium angustitubum *with photograph (by L Nanyeni) of individual vouchered as Nanyeni 862.*

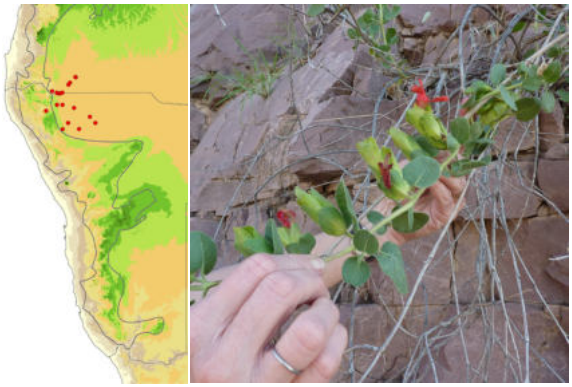

Figure 26: *Occurrences of* Petalidium bracteatum *with photograph (by L Nanyeni) of individual vouchered as Nanyeni 4054.*

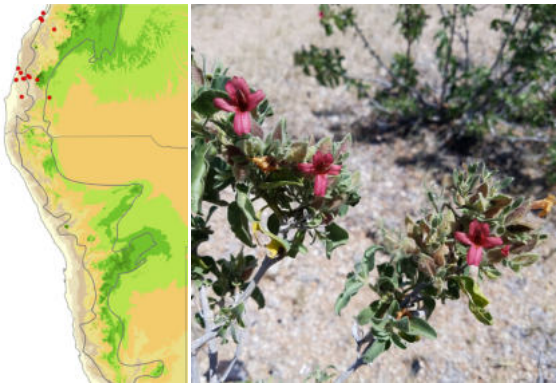

Figure 27: *Occurrences of* Petalidium glandulosum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 6926.*

HEAN endemics

Petalidium kaokoense Swanepoel: This is a recently described species that is distinguished by its stout base and white peeling bark. It has a very restricted distribution in the Hartmann Mountains and nearby areas to the east (Figure 28).

HEAN near-endemics

Petalidium cirrhiferum S.Moore: This species is distinct among *Petalidium* in having a toothed, crenulate leaf margin (Figure 29). Within this group, it is distinct in having flowers that tend towards a deep purple-pink colour rather than maroon. The species occurs near the Cunene River where the river traverses the highlands and escarpment, but also eastwards and westwards of the HEAN.

Petalidium sp. nov. Dexter & Tripp 7296: This is a recently discovered, putatively novel species that requires further study. It is similar to *P. physaloides* (Figure 31) in its flowers, but forms larger, more robust plants, with a stout base similar to *P. kaokoense* (Figure 28). It is only known from a population found near the entrance to Iona National Park in Angola, on the western edge of the HEAN (Figure 30). At present, we consider it too data deficient to determine if it is an endemic of the HEAN or not.

Other species not associated with the HEAN

Petalidium physaloides S.Moore: This species is similar to *P. kaokoense* (Figure 28) and *P.* sp. nov. Dexter & Tripp 7296 (Figure 30), but it has a more delicate growth form with spindly, ascending branches

Figure 28: *Occurrences of* Petalidium kaokoense *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 4075.*

(Figure 31). While there are multiple records from Namibia, we believe these are misidentifications and that the species is restricted to Angola, where it occurs primarily in the coastal plain west of the highlands and escarpment.

5. Minute-, maroon-flowered group

The species in this group are characterised by minute maroon flowers with yellow nectar guides, similar to that of *P. physaloides* (Figure 31), but smaller. Only *P. setosum* (Figure 34) has a flower that approaches the size of those in the previous group. Also, the species in this group have congested inflorescences, forming a sub-woody (*P. setosum*) or woody 'head-like' structure (*P. halimoides, P. lanatum* and *P. lepidagathis*; Figures 32, 33 and 35, respectively). Species tend to be prostrate (except *P. setosum* that can be more upright) and some grow extensively via runners (*P. ramulosum* and *P. tomentosum*; Figures 36 and 37). No species in this group is endemic to the HEAN.

HEAN near-endemics

Petalidium halimoides (Nees) S.Moore: This species (Figure 32) is very similar to *P. lanatum* (Figure 33) in its prostrate growth form with inflorescences in woody heads. It only seems distinguishable by a deltoid leaf shape with a flat base, while *P. lanatum* has more elliptic leaves with the base attenuate on the petiole. Intermediate forms have been observed. These two species have parapatric distributions across the HEAN, with *P. halimoides* occurring in northern Namibia and on the coastal plain in southern Angola.

Petalidium lanatum (Engl.) C.B.Clarke: See the previous species (*P. halimoides*) for morphological limits of this species. It occurs in the highlands, escarpment and coastal plain of central Namibia (Figure 33).

Petalidium setosum C.B.Clarke ex Schinz: This species is distinguished from others in the group in its larger, more upright growth form and its larger flowers (Figure 34). Vegetatively and in the form of the inflorescence, it is very similar to *P. canescens* (Figure 15), but the flowers are clearly distinct. It has one of the widest latitudinal distributions of any species of *Petalidium* but is largely restricted to the highlands and escarpments of Namibia and neighbouring areas to the east and west.

Other species not associated with the HEAN

Petalidium lepidagathis S.Moore: The inflorescence of this species (Figure 35) is very similar to that of *P. halimoides* and *P. lanatum* (Figures 32 and 33, respectively), but the leaves are much more lanceolate and nearly linear (Figure 35). It is primarily found on the coastal plain in southern Angola. It has a parapatric distribution with respect to *P. halimoides*, and we have observed putative hybrids, assessed on morphology, where their ranges meet.

Petalidium ramulosum Schinz: This species (Figure 36) and *P. tomentosum* (Figure 37) are characterised by long rooting runners, but they have completely non-overlapping distributions. The leaves are glaucous and covered in dense pubescence similar to

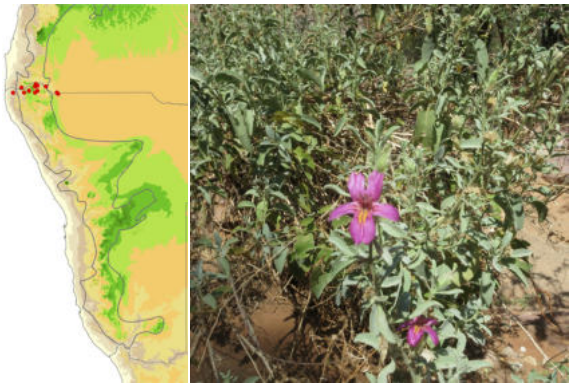

Figure 29: *Occurrences of* Petalidium cirrhiferum *with photograph (by K Dexter) of individual vouchered as Dexter 7489.*

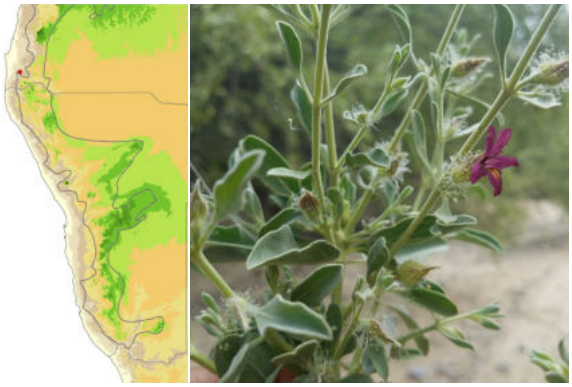

Figure 30: *Occurrences of* Petalidium *sp. nov. Dexter & Tripp 7296 with photograph (by K Dexter) of individual vouchered as Dexter 7296.*

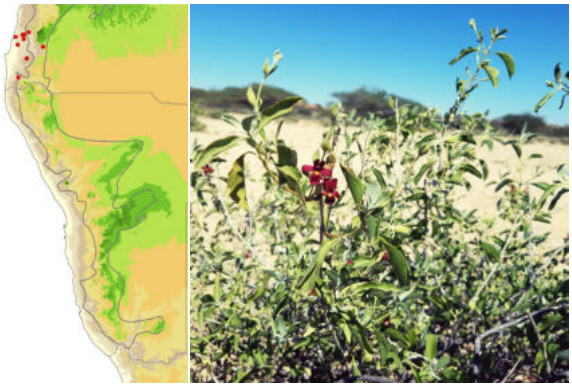

Figure 31: *Occurrences of* Petalidium physaloides *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 6954.*

Figure 32: *Occurrences of* Petalidium halimoides *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 6943.*

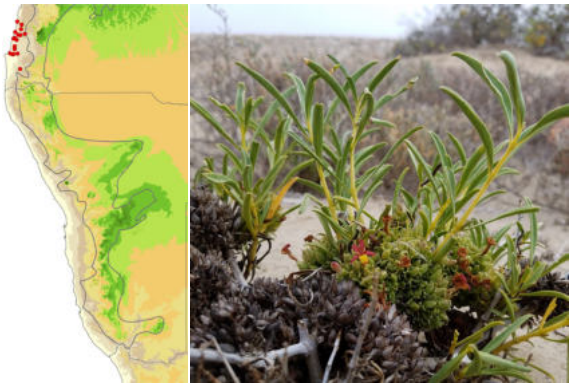

Figure 35: *Occurrences of* Petalidium lepidagathis *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 6941.*

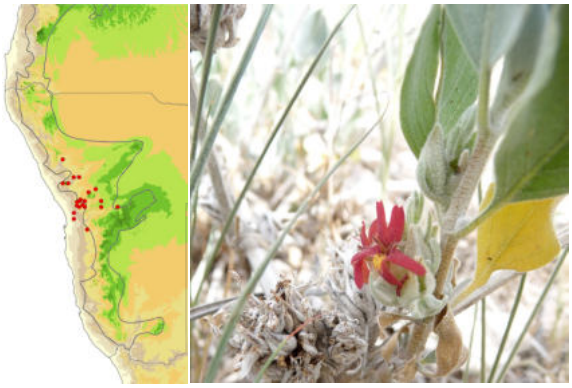

Figure 33: *Occurrences of* Petalidium lanatum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 833.*

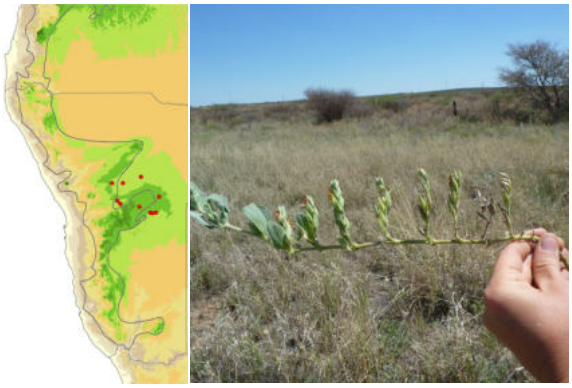

Figure 36: *Occurrences of* Petalidium ramulosum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 4120.*

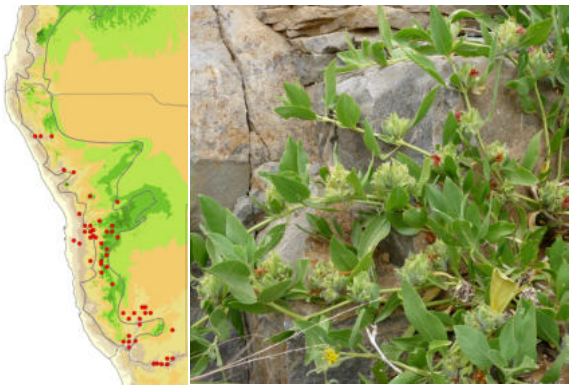

Figure 34: *Occurrences of* Petalidium setosum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 887, growing upwards at base of cliff .*

Figure 37: *Occurrences of* Petalidium tomentosum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 6928.*

P. englerianum (Figure 20). This species occurs primarily east of the highlands in central Namibia.

Petalidium tomentosum S.Moore: This species has the smallest leaves of any *Petalidium* and grows in a completely prostrate form under very arid conditions where few other woody plants can grow. It is largely restricted to the coastal Namib Desert in Angola (Figure 37).

DISCUSSION

Sixty-one per cent of African species of *Petalidium* (22 of 36) are endemics or near-endemics of the central and southern portions of the highlands and escarpments of Angola and Namibia (HEAN). Coupled with our knowledge that all 36 species of *Petalidium* in Africa arose in the last 1.6–4.3 million years (Tripp *et al*. 2017, Loiseau *et al*. 2023),

our results here suggest that the highlands and escarpments in this area have played a key role in plant speciation and generating biodiversity. While there is certainly value to focusing conservation efforts on unique and species-poor evolutionary lineages (e.g., giant pandas, tuataras or *Amborella*), it can be considered equally imperative to focus on lineages such as *Petalidium*, which show great evolutionary lability and are undergoing evolutionary radiation. It is these radiating lineages that may present the greatest evolutionary potential in the face of environmental change (Eizaguirre & Baltazar-Soares 2014). Moving beyond academic debates on the conservation value of 'old' versus 'young' species, our contribution, which reports a high number of endemic species in the highlands and escarpments of Namibia and southern Angola, clearly shows the value of the area for plant conservation.

We may have a better understanding of species distributions for *Petalidium* than for many other plant lineages in the HEAN, but this does not mean we understand those distributions very well. Many areas of the HEAN are remote and hard to access, particularly because of challenges posed by water access when working far from roads (and thus vehicles which carry water). Nevertheless, these remote areas need to be explored. Given that many species of *Petalidium* show very restricted distributions, we are confident that more species in the genus will be documented as more botanists visit remote areas of Namibia and Angola. Collaboration with local residents, indigenous or otherwise, could aid in this effort as our personal observations have clearly shown the ability of local people to identify different species of *Petalidium*.

The recency of speciation in *Petalidium* is a double-edged sword, leading to challenging taxonomy but great opportunities for understanding plant evolution and speciation. More taxonomic work is clearly needed to understand the morphological limits of species and define conservation agendas going forward. Beyond taxonomy, we advocate for further evolutionary studies of *Petalidium*. It presents an ideal model system for plant evolutionary research, including studies of hybridisation, a process increasingly recognised as fundamental to plant evolution (Schley *et al*. 2022). In *Petalidium*, species boundaries may be incompletely formed given recent speciation, which allows for the possibility of hybridisation. We have observed multiple putative hybrids in the field, including populations that appear to represent 'mixes' of two identifiable progenitor species that are also present in the landscape. We also sometimes find populations of *Petalidium* where the vegetative morphology suggests one species and the floral morphology an entirely different species (see *P. subcrispum* (Figure 14) and *P. englerianum* (Figure 20), for example). These may be hybrid origin species and are an exciting avenue for future research.

A frequent goal of systematic and evolutionary studies is to produce a complete DNA sequence-based phylogeny of the group of species under study. This is a goal we are actively striving for with *Petalidium*, building on our previous work (Tripp *et al.* 2017, Loiseau *et al*. 2023). However, if hybridisation is common in the group, reticulate evolutionary patterns may also be common, and a single, 'correct' topology may not exist. Nevertheless, more DNA sequence data from more populations of more species will only advance our evolutionary understanding of the genus.

Petalidium is remarkable in the variety of floral forms of its species, particularly given the young age of the genus (maximum of 4.8 Ma; Tripp *et al*. 2017), and we have suggested above that this is due to adaptation to different pollinators, such as bees, sunbirds and long-tongued flies. However, we have only undertaken cursory pollinator observations in the field, and no quantitative studies of pollination biology have been carried out in the genus. Such quantitative studies, via direct observations or camera-trapping, would greatly increase our understanding of the potential role of pollinators in interspecific pollen transfer and are needed to inform on which animal species may be dependent on different species of *Petalidium*.

Petalidium offers an excellent opportunity to understand plant adaptation in arid environments. It achieves remarkably high abundance in regions that are particularly challenging for woody plants, due to low annual rainfall and high interannual rainfall variability. *Petalidium* can blanket entire valleys where it rains less than 100 mm a year on average and, in some years, it does not rain at all. How do species of *Petalidium* survive in such dry conditions? Preliminary anatomical studies of leaves suggest adaptations to arid environments (E. Manzitto-Tripp *et al*. unpubl. data), which may play a role in making photosynthesis more efficient, allowing plants to minimise the opening of stomatal pores and consequently reduce water loss. We have also observed in the field that multiple, to almost all, branches of a given *Petalidium* individual may die back but that resprouting can occur with vigour when water availability allows, demonstrating another plant strategy to deal with drought (Craine 2009, Folk *et al*. 2020). Some species of *Petalidium* may be deciduous, to allow cessation of water loss during dry periods, but further fieldwork is needed to confirm which exact species carry this trait. Ecophysiological studies are needed to study the multiple mechanisms that may allow *Petalidium* to prosper in hyperarid regions.

Lastly, species of *Petalidium* need research from a conservation perspective, beyond simple geographic studies of their distribution as done here. We recently undertook fieldwork on *Petalidium* in northwestern Namibia (April–May 2022) in areas that we visited a decade earlier during four field visits (2010–2013). In revisiting some of the same populations, we documented astounding declines in abundance. In some places, one could see numerous standing dead shrubs of *Petalidium*. In others, we could find no trace of previously collected populations. Is this due to the exceptionally dry conditions between visits, to overgrazing (particularly by goats) or a combination of the two? Interestingly, in areas where we previously documented multiple genera of Acanthaceae, *Petalidium* was greatly reduced in abundance, but *Dinteracanthus* C.B.Clarke ex Schinz, *Monechma* Hochst. and other genera seemed to be fine. Are species of *Petalidium* particularly tasty to herbivores (native or non-native)? Are human populations, and thus goat and other livestock populations, increasing in the region? Have management practices and grazing areas changed? Many of these questions could be addressed with existing data or simple field studies. Answering these questions would help us to understand the threats to species of *Petalidium* and to plant populations in general in these arid highland and escarpment areas. Such applied research is urgently needed.

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