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Front cover: *C. bachelorum* on quartzite blocks on a hilltop southwest of Steinkopf.

Photo: Chris Rodgerson

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Back cover: *C. subterraneum* near Eksteenfontein in the Richtersveld.

Photo:Andrew J. Young

Contents

The dwarf succulent genus *Conophytum* N.E.Br.: distribution, habitat and conservation.

Andrew J. Young and Chris Rodgerson

Abstract

The dwarf succulent genus *Conophytum* N.E.Br. is one of the most species rich in the Aizoaceae. Primarily restricted to the arid winter-rainfall region of the Northern and Western Cape Provinces of South Africa and southwestern Namibia, the genus is most closely associated with the Succulent Karoo biome, a region of high floral endemism and biodiversity. Many taxa are niche-specialists and almost a third of all *Conophytum* are severely range-restricted and can be considered to be point-endemics. The genus as a whole is vulnerable to anthropogenic impacts and many species are threatened by activities such as mining, agriculture and climate change.

Introduction

The result of a very recent radiation event (Klak *et al.* 2004; Valente *et al.* 2014) *Conophytum* displays a remarkably high degree of speciation with 165 species and subspecies (together with a number of varieties) recognised (Hammer & Young 2017). Plant form varies and several morphologically sections have been defined in *Conophytum* as a result (Hammer 1993, 2002; Hammer & Young 2017). Along with CAM-photosynthesis (Crassulacean Acid Metabolism) the miniaturisation of growth form in leaf succulents such as *Conophytum* is one of several adaptations their arid environment. This article considers the distribution of this genus in southwestern Africa in the context of their habitat and looks at implications for their conservation.

Distribution

Conophytum is strongly associated with the winter-rainfall region of South Africa and Namibia, and especially the Succulent Karoo biome (Fig. 1). More than 93% of *Conophytum* taxa are recorded from this biome alone, with many of the remaining taxa located on the biome's immediate fringes and often in the transitional area at the boundary of winter- and summer-rainfall areas (Young & Desmet 2016). A recognised global biodiversity hotspot and one of only two entirely arid hotpots (Cowling *et al.* 1998; Mittermeier *et al.* 2004), this biome is characterised by a high degree of floral endemism, especially in dwarf-leaf succulents (Driver *et al*. 2003; Mucina *et al*. 2006a). Such endemism is a strong characteristic in *Conophytum* and is reflective of the high speciation seen in the genus. Approximately 60% of taxa are only found in the Succulent Karoo biome. The Namaqualand Hardeveld bioregion is most important in terms of both taxon richness and endemism and, as such, is consistent with the pattern seen in the flora as a whole (Snijman 2013). Species richness and endemism (Table 1) is also high in the Richtersveld bioregion. By contrast, the level of *Conophytum* endemism in areas such the Knersvlakte bioregion is low by comparison to that seen in other flora. At a smaller scale, the Namaqualand Klipkoppe Shrubland vegetation unit is the most species rich with 66 *Conophytum* taxa) present. It is also home to most endemics (23 taxa) and most point endemics (14). Some of the smaller vegetation units, especially within the Richtersveld bioregion, are also surprisingly species rich (Young & Desmet 2016). In terms of species richness a clear pattern is evident so that the area around the Namaqualand town of Springbok can be considered as '*Conophytum*-central' (Fig. 2.) This is generally a florally diverse area characterised by the presence of multiple vegetation units, the majority of which possess *Conophytum* taxa. Further away from here, species richness falls away

Most of the Succulent Karoo is characterised by low and rather unpredictable levels of rainfall in the winter months (Desmet & Cowling 1999a), and it is in these parts of the biome that the genus predominates. *Conophytum* is much less common, and may be absent, in the eastern parts of the biome that experience year-round or bimodal rainfall patterns (e.g. in the Trans-Escarpment Succulent Karoo and the Rainshadow Valley Karoo; Bradshaw & Cowling 2014). *Conophytum* is absent from the predominantly summer-rainfall Karoo centre, and fewer than 15% of taxa are found within the Cape Floristic Region where the amount of rainfall rather than its seasonality is thought to be a limiting factor. The role of non-rainfall moisture is almost certainly a vital element in sustaining dwarf succulents such as *Conophytum*. Fog probably makes the most substantial and reliable contribution to total moisture, especially on the west coast but it may also be significant further inland (Matimati *et al.* 2012). Such events are typically highly localised and can strongly influence the distribution of *Conophytum* in terms of niche preferences. Geology is very significant in the distribution of the genus with separate taxa showing distinct preferences for sandstone, granite, gneiss and especially quartz (Hammer 1993; Young *et al*. 2016). Figures 3-6 illustrate some of the habitat preferences for *Conophytum* species on these substrates.

While the vast majority of species are found in South Africa, data for Namibia remains relatively poor. Just six *Conophytum* taxa are endemic to Namibia with a further ten taxa found within the country where they are most abundant on the hills

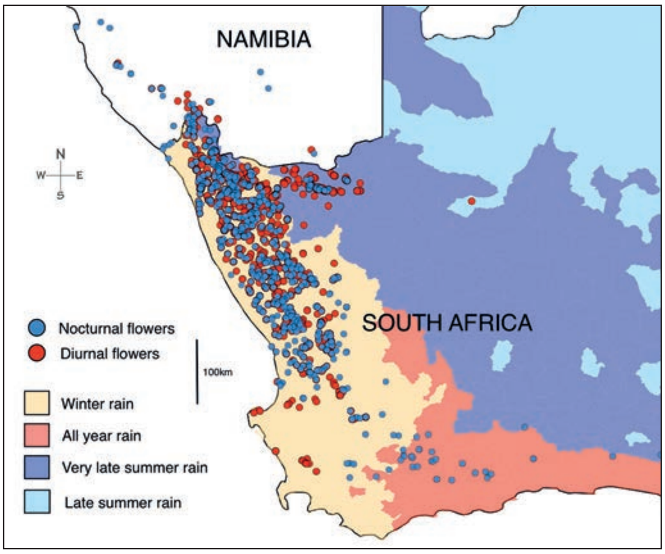

Figure 1. A map of southwestern Africa showing the distribution of diurnal- and nocturnal-flowering *Conophytum* species and subspecies. For South Africa the seasonality of rainfall, a critical factor in the distribution of the genus (Young *et al*. 2016), is highlighted (redrawn from Schulze & Maharaj, 2007).

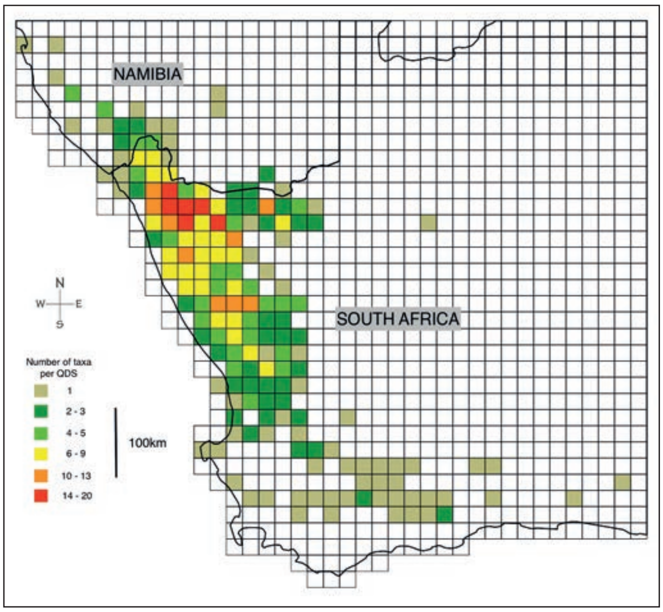

Figure 2. A map of southwestern Africa showing the distribution of *Conophytum* taxa (species and subspecies) per quarter degree square. This has been produced from the *Conobase* – a database consisting of more than 3,000 unique locality records for the genus (updated from Young & Desmet, 2016).

and mountains close to the Orange River, on rocky outcrops amongst the fog-belt along the coast (as far north as Lüderitz) and on the numerous inselbergs of the restricted diamond zone, the Sperrgebiet. Arguably more so than taxa further south *Conophytum* species in Namibia display a high degree of niche specialism, seeking out often small patches of shelter and moisture.

The Succulent Karoo shares boundaries with the Desert, Nama Karoo, Fynbos and Albany Thicket biomes and *Conophytum* taxa are found in all of these except the latter (Young & Desmet 2016). In the Nama Karoo a greater unpredictability or variability in rainfall oriented to a summer phenological peak (Desmet & Cowling 1999a) results in a biome that is not florally rich and lacks a centre for endemism (Cowling *et al.* 1998; Mucina *et al.* 2006b; Van Wyk & Smith 2001). *Conophytum* follows this pattern with just a handful of taxa and only a single endemic (in Namibia) recorded from the biome. The occurrence of *Conophytum* in the Nama Karoo is always in association with habitats or vegetation types that are still under the influence of the winter-rainfall systems. This is especially prevalent in the Bushmanland Inselberg Region where the topography supports isolated outliers of Succulent Karoo vegetation units. By contrast to the Succulent Karoo, the Desert biome generally affords rather sparse vegetation cover. Rainfall is highly variable and displays a marked west-east transition (Jürgens 2006). Temperatures are extremely high and variable. Fog can play a key role as a critical source of moisture. Floral endemism is most prevalent along the Orange River and the mountainous desert section of the Richtersveld region which experience exposure to low levels of winter rainfall together with local fogs (Jürgens 1991, 1997). Once again this is reflected in the distribution of the genus *Conophytum*, with the plants often occupying niche, moisture-trapping, habitats. In stark contrast to the overall species richness of the Fynbos biome (especially the Renosterveld vegetation complex, Rebelo *et al.* 2006) surprisingly few *Conophytum* taxa are recorded, with just seven taxa endemic to the biome (Young & Desmet 2016).

A strong feature of the genus is its geographical fragmentation into spatially isolated taxa, often with a highly restricted distribution. In *Conophytum* the area of occupancy for some species may sometimes be just a few hundred square metres. Examples of point endemism in *Conophytum* are especially common within the Succulent Karoo, and account for ~28% of taxa. Such localities may include mountains (e.g. *C. cubicum* on Black Face Mountain), inselbergs (e.g. *C. achabense* on Achab), small hills (e.g. *C. schlechteri* on Farquharson-se-kop), quartz ridges (e.g. *C. regale* north of Springbok) or quartz gravel flats (e.g. *C. burgeri* at Aggeneys). It is worth noting that whilst the geographical range of the majority of *Conophytum* taxa is generally restricted, a few species (e.g. *C. bilobum* and *C. pageae*) have a latitudinal range that can extend hundreds of kilometres.

Flowering

In a majority of *Conophytum* taxa flowering is diurnal with far fewer species flowering at night (Fig. 1). In some taxa, though, the distinction between day and night flowering is less evident (Hammer 1993). Pollination itself appears to be non-specialist, largely relying on months and pollen wasps for nocturnal and diurnal flowering taxa, respectively (Jürgens & Witt 2014). As such, this would not appear to be a significant limiting factor in the distribution of the genus. Although pollination in the genus appears to be non-specialist (Jürgens & Witt 2014), incidences of natural hybrids are relatively uncommon in *Conophytum*, even in areas of high species richness. The best example of a natural hybrid occurs near the town of Springbok, where dense colonies of *C. ectypum* ssp. *brownii* (magenta flower) regularly hybridise with the less (locally) abundant *C. bilobum* (yellow flower) in the form of *C.* × *marnierianum* with red and orange flower forms (which now appears to have stabilised at the eastern edge of a quartz ridge). Because of the common flowering times it is not understood why such hybridisation is only rarely observed. In some localities, different species may be vertically separated on a hillside. Similarly point endemism in the genus suggests that pollinators operate over short distances. Subsequent seed dispersal is probably very localised, contributing perhaps to incidences of point-endemism, but again this is poorly understood. In much of the distribution range it is common to find a nocturnal and diurnal flowering species growing close together. The absence of day-flowering taxa from the south-eastern extent of the distribution of the genus (e.g., in the Klein Karoo) is notable but the reasons for this not understood.

An important characteristic of the genus is that, with the exception of a handful of taxa, flowering displays a temporal shift compared to the vast majority of the Aizoaceae. The vast majority of *Conophytum* taxa flower in the austral autumn with fewer in the spring. Jürgens and Witt (2014) suggested that the frequency of nocturnal flowering (accounting for 25% of taxa) is a result of this temporal separation from other, closely-related, genera. There does not appear to be any particular influence or association governing the distribution of those *Conophytum* taxa that display 'out-of-season' flowering (i.e. in spring or summer). Interestingly, there are a handful of examples in which discrete 'pairs' of morphologically-similar taxa that lie within just 2–3 kilometres to each other flower in different seasons: one in the austral autumn and the other in the spring (e.g., *C. confusum* and *C. bachelorum*; Young *et al.* 2016).

Habitat

Conophytum occupy a wide range of habitats and a preference for different geologies, including the sandstone of the Bokkeveld plateau, the quartz-pebble–rich plains of the Knersvlakte, the high granite-dominated mountains of the Khamiesberg and the quartz inselbergs of Bushmanland and the southern Namib

Figure 3a–c. Some *Conophytum* taxa succeed among small quartz stones on open vlaktes which provide a stable growing environment. The tightly packed white quartzite provides cooling shelter from intense summer heat by reflecting strong sunlight. It also gives protection and sustenance by trapping available moisture and filtering light to allow seeds to germinate and seedlings to survive. Many of the species in these areas are subterranean, retreating sub-surface during the summer. (a) *C. calculus* ssp. *calculus* with its pale, highly fused leaf pairs in the Knersvlakte. (b) *C. ratum* at the Gamsberg (a quartz inselberg in Bushmanland that is currently being mined). This species is mostly buried with only the windowed upper part visible (approx. 1cm diameter) above ground (c, back cover) *C. subterraneum* near Eksteenfontein in the Richtersveld.

Figure 4a–c. The very tops of quartzite hills and mountains also provide many *Conophytum* with the moisture they benefit from as a result of frequent exposure to fogs and low clouds browsing the peaks. Some species prefer the gravels which accumulate on the flatter areas on top of these peaks, but most prefer to occupy the smallest of cracks and fissures in large rocks and boulders where they do remarkably well in these seemingly nutrient-free places. Invariably restricted to the south and southwest shadier sides of hills, seeds lodge and germinate in such niches deep inside theses cracks and again, the stability of their micro-habitat appears to be a key factor in their success. (a) *C. stephanii* ssp. *helmutii* inhabiting vertical cliffs on the massive Rosyntjieberg in the Richtersveld. (b) *C. tantillum* ssp. *amicorum* at its only known locality on a small quartzite hill north of Springbok. (c, front cover) *C. bachelorum* on quartzite blocks on a hilltop southwest of Steinkopf.

5a

5b

Figure 5a–c. Granite or gneiss formations (often referred to as domes) are a favoured habitat for many *Conophytum* taxa. They are regularly covered with weathered depressions or 'pans' just a few millimetres deep which fill with fine detritus and are subsequently occupied by *Conophytum* if the depth and aspect are favourable. When it rains these pans will flood with water for a few days until it evaporates. Other domes may be of the exfoliating type, where often huge plates of rock can fissure and detach from the main bulk but remain stable due to their size and weight. These produce over-hanging 'lips' where detritus can accumulate below, allowing seeds to germinate and grow on within their protection as it gives the shade and moisture required. Aspect is also important and very often the less exposed south and southwest sides of such domes accumulate a layer of lichen and moss. These in turn may provide a micro-habitat of detritus and moisture and an anchor for the roots which many *Conophytum* species thrive in. (a) *C. depressum* ssp. *depressum* in a shallow grit pan on top of a gneiss dome. (b) *C. youngii* retreats deep inside its lichen host during the heat of summer but luxuriates within its protection during fall and winter. (c) *C. pellucidum* ssp. *pellucidum* under the lip of an exfoliating granite dome.

5c

Desert. The highest levels of floristic species diversity within the region, especially amongst dwarf succulents, are often associated with koppies or rocky outcrops, which are often small in extent or isolated (Desmet & Cowling 1999b). This is also where we find many, but by no means all, *Conophytum* taxa. These plants are rarely found in large or dense communities but are rather widely dispersed amongst other succulent shrubs or occupy discrete habitat niches, for example, small rocky outcrops in large sandy plains, the edges of shallow grit pans, shaded (typically south-facing) lichen-covered granite slopes or on flat gravel plains. Examples of the different habitats where *Conophytum* are primarily found are given in Figs. 3–6). The area occupied by many populations is often very small, to the extent that small, isolated, populations may be easily overlooked. Whilst granite, gneiss, sandstone and, especially, quartz are the most important geologies (the quartz content of such gneiss and sandstone is often notable), *Conophytum* are occasionally found on shale (e.g., *C. pageae*), limestone (e.g., *C. uviforme* ssp. *subincanum*) and calcrete (e.g., *C. caroli*).

Conservation

The major threats to succulents such as *Conophytum* are well recognised: agriculture (notably viniculture and rooibos plantations but also grazing and trampling by livestock), road building, illegal collection, mining and quarrying. Currently, fewer than a third of *Conophytum* taxa are protected within existing formal conservation areas such as the Knersvlakte. Even once all informal reserves and focus areas identified by the National Protected Areas Expansion Strategy are included, approximately one quarter of all *Conophytum* taxa would remain outside any protection. Point endemics are already, by definition, highly vulnerable and given the high level of such endemism within the genus this is a concern. A recent reassessment of the genus for the South African National Red List by one of us (AJY) determined that more than half of all *Conophytum* taxa (to varietal level) are currently threatened, i.e., fitting one of the IUCN categories of critically endangered, endangered or vulnerable or the National categories of critically rare or rare (South African National Biodiversity Institute, 2016). An example of one such critically endangered species is *C. ratum* (Fig. 3b) for which the only substantive population of plants is located on the Gamsberg, a quartz inselberg in Bushmanland. This inselberg is currently being mined for its zinc deposits, threatening the unique flora of this mountain.

Despite the clear threat proposed, such Red List assessments do not currently take into account the potential harm posed by anthropogenic climate change (this is now being considered by the IUCN). A recent modelling study indicated that up to 80% of current habitat occupied by *Conophytum* may be lost over the next few decades due to changes in our climate (Young *et al.* 2016). This would result in a high risk of extinction for a majority of *Conophytum* taxa although the most species rich area (the Namaqualand Hardeveld bioregion) appears to be less adversely affected than others and has the potential to act as a refuge in future. However, as we have seen above, *Conophytum* is a genus that relies on localised conditions, particularly those governed by geology, exposure (aspect) and, especially, moisture availability. But we simply do not know enough about the overall contribution made by local moisture events such as fog and how these might be affected by climate change.

Table 1. Presence of *Conophytum* taxa (species and subspecies) in the bioregions of South African Biomes.

Biome	Bioregion	Number of individual taxa	Proportion of total *Conophytum* taxa represented in the bioregion (%)	Number of taxa endemic to the bioregion	Proportion of total *Conophytum* taxa endemic to the bioregion (%)
Desert	Gariep Desert	32	20.1	4	2.5
	Southern Namib Desert	8	5.1	0	0
Fynbos	East Coast Renosterveld	1	0.6	0	0
	Eastern Fynbos Renosterveld	1	0.6	0	0
	Karoo Renosterveld	4	2.5	0	0
	Namaqualand Cape Shrublands	9	5.7	0	0
	Northwest Fynbos	11	7.0	3	1.9
	Southwest Fynbos	2	1.3	0	0
	West Coast Renosterveld	2	1.3	0	0
	West Strandveld	4	2.5	0	0
	Western Fynbos Renosterveld	4	2.5	0	0
Nama Karoo	Bushmanland	22	13.8	0	0
	Lower Karoo	1	0.6	0	0
Succulent Karoo	Knersvlakte	11	6.9	3	1.9
	Namaqualand Hardeveld	84	53.2	43	27.0
	Richtersveld	67	42.4	24	15.7
	Namaqualand Sandveld	15	9.5	2	0
	Trans-Escarpment Succulent Karoo	6	3.8	0	0
	Rainshadow Valley Karoo	10	6.3	4	2.5


6a


6b

Figure 6a–c. Weathered sandstone is another favoured habitat for many species in the genus. Many *Conophytum* taxa thrive on the Bokkeveld and Cederberg sandstones where they inhabit shallow sandy pans and lichen and moss-covered rocks. The edges of the high sandstone plateaus and escarpments such as the Matsikammaberg benefit from regular moisture provided by low clouds and fogs, sustaining many miniature succulents including *Conophytum*. Sometimes the plants will inhabit only the shallow fringes of a large and deeper pan and just like the pans on granite domes, sandstone pans must be level and just the correct depth for conophytums to make use of them. Many pans may look just right but if the depth is too little or too great or there is any incline they are generally devoid of such plants. (a) *C. minusculum* ssp. *minusculum* '*paucilineatum*' in a weathered sandstone 'pocket' among rooibos plantations south of Clanwilliam. (b) *C. minusculum* ssp. *minusculum* finds the protection of thick, dark moss to provide the ideal environment on the north-eastern end of Matsikammaberg. (c) *C. obcordellum* ssp. *obcordellum* '*ursprungianum*' in a shallow sandstone grit pan south of Nieuwoudtville.


6c

Conclusions

The genus *Conophytum* is a remarkably diverse and successful group of plants, well adapted to their environment, often seeming opportunistic in their colonisation and subsequent exploitation of niche habitats. Despite their adaptive capabilities, many taxa within the genus are under immediate or future threat. Overall, studies such as this may help identify a potential refuge area and inform conservation opportunities. On a more positive note, *Conophytum* taxa continue to be discovered but it is worth noting that none of the new species discovered in the last 20 years or so have extended the known range of the genus. Most have been found in areas of existing high biodiversity in the Succulent Karoo (e.g. *Conophytum smaleorum* in the southern Richtersveld) and several have been found in close vicinity to towns and even within sight of major highways, including the N7. There remains much work to be done in terms of exploration including, rather intriguingly, several historical records in the northeastern extent of the genus's distribution (along the Orange River and towards Upington) which have eluded botanists since the mid-1930's.

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