Conophytum bachelorum and its relatives: the introduction of a new *Conophytum* from Namaqualand, *C. confusum*.

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Photographs by the authors.

Summary: A reassessment of a group of four closely related taxa of the dwarf succulent genus *Conophytum* from Namaqualand, South Africa has been undertaken. This has resulted in the description of a newly discovered taxon, namely *Conophytum confusum*.

INTRODUCTION

The specific environmental conditions in the Succulent Karoo biome that lies within the Northern and Western Capes of South Africa and the southwest corner of Namibia have resulted in a unique flora well adapted to those conditions. The resulting flora is dominated by a large number of leaf succulents, notably members of the Aizoaceae and Crassulaceae (Cowling and Hilton-Taylor, 1999). The biome is strongly species-rich with approximately 5,000 vascular plant species and, even amongst such a large and diverse a group such as the Aizoaceae, the genus *Conophytum* shows a remarkable degree of speciation (with >160 taxa now recognised at the level of species or subspecies, Hammer and Young, 2015). The flora of the biome is also characterised by high levels of range-restricted endemism (Cowling and Hilton-Taylor, 1994; Hilton-Taylor 1996). Such localisation of individual taxa, often restricted to a single, sometimes geographically isolated, location (see Ihlenfeldt, 1994; Desmet et al. 1998) is very pronounced in *Conophytum,* in which ~28% of all taxa can be considered to be point-endemics (unpublished). The miniaturisation of growth form in leaf succulents such as *Conophytum* is an adaptation unique to the region and most evident in the Succulent Karoo biome (Desmet and Cowling, 1999). The greatest floral species diversity, especially in dwarf succulents, is often associated with koppies or rocky outcrops (typically quartz or gneiss; Desmet and Cowling, 1999). *Conophytum* is no different in this regard, with plants occupying niche environments on a variety of rock surfaces across its full geographical range (flats, slopes and vertical surfaces) of different geologies (especially granite, quartz, sandstone and gneiss) and aspects (ranging from deep shade to full sun).

The continued hunt for new *Conophytum* populations through regular field trips to Southern Africa rarely fails to surprise, often turning up new (sometimes disjunct) populations and long-lost or undiscovered species. The high incidence of point endemism seen in the genus means that there are often small numbers of plants in an area so small (e.g., *C. youngii* occupies an area < 1,000m^2) that they may be easily overlooked – walk a few metres one way or another and one can pass them by, oblivious to their existence. When two of the authors went to observe *C. bachelorum* in habitat in the knowledge that as at least six other botanists had preceded them they did not really expect to find anything new. What was found resulted in a degree of uncertainty amongst experts on the genus for some years and strongly influenced the eventual naming of a new taxon. Importantly the observations made also led to a full re-evaluation of four closely related *Conophytum* taxa.

DISCOVERY

In April 2008 two of the authors (AJY & CR) set out from the Northern Cape town of Springbok with the intention of seeing *C. bachelorum* in habitat. This rare and rather elusive *Conophytum* is known only from a semi-remote and somewhat difficult to access quartz ridge lying to the NW of the town (Figure 1). The ridge itself is unremarkable (Figure 2) and typical in terms of both geology and general succulent flora of the area. *C. obscurum* was the dominant *Conophytum* on the lower slopes (and absent from the top of the ridge) whilst *C. meyeri* was abundant along the top of the quartz ridge. Both *C. meyeri* and *C. obscurum* are widespread across the quartz hills in the area. Such vertical stratification of *Conophytum* taxa is common on hills in Namaqualand. Whilst on his hands and knees with camera and tripod taking a photograph of *C. meyeri* in full flower, AJY noticed a second *Conophytum* scattered amongst the quartz (Figure 3). This turned out to be a small population of plants (<1000) that resembled *C. bachelorum* morphologically (Figures 4-5). Unlike both *C. meyeri* and *C. obscurum* these plants were not in flower. This seemed to be consistent with the behaviour of *C. bachelorum* as it flowers several months later in the year (typically in late August/September). However, upon close examination it was clear that the flower remains on large numbers of plants were only a few days old indicating that flowering had just finished. This was completely unexpected so just what was going on here? Were these actually *C. bachelorum*? The resulting confusion about the identity of these plants influenced the subsequent naming of the taxon.

In 2008 we did not, however, take the opportunity to explore the full extent of the quartz ridge – a mistake that ultimately necessitated a second visit to the area. Had we done so we would have realised that this was not the only such population on the ridge. On the subsequent visit three years later, timed to coincide with the known flowering period of *C. bachelorum* (in September) we traversed the entire length of the quartz ridge (approx. 3 km). In doing so we discovered that there were two quite separate populations of morphologically similar plants less than 2km apart. But there were differences between these two populations of plants. First, it was clear that the niche habitats they occupied differed (see below). Second, the flowering of these plants was temporally separated.

In this second, larger, population the vast majority of plants were in full flower in September, consistent with the expected behaviour of *C. bachelorum* (Figures 6-7). On our return to the UK we were also able to confirm that the location of this second population matched the details provided to us for what we understand to be the Type locality of *C. bachelorum* by two other botanists who had visited the site in recent years. By contrast, the plants we first observed in 2008 on the eastern end of the ridge were out of flower at that time of year and completely lacked flower remnants. This would be in keeping with an autumnal flowering period (April-May). Both *C. bachelorum* and the new taxon appear to be endemic to that particular quartz ridge and field work by the authors and others has failed to detect any further populations on nearby hills (that possess a similar geology).

Other flora on the ridge included *C. meyeri*, which was sympatric with the population of *C. confusum* but was absent from the immediate habitat of *C. bachelorum*. Much further along the ridge, we found scattered individuals of two additional *Conophytum* species, namely *C. stevens-jonesianum* (nocturnal flowering) and *C. bilobum*. *Adromischus marianiae* var. *herrei* was also notable from the same ridge, growing amongst small shrubs or in the cracks and fissures of large quartz blocks, often in close association with *Conophytum* taxa (Figure 8).

Less than 30km away from this ridge on another quartz hill a remarkably similar juxtaposition of two similar *Conophytum* species occurs. CR and AJY visited this second site in August 2014 in order to observe its two endemic species in habitat. Here, a very small population (<1000 plants) of the tiny, single-headed *C. chrisolum* occupies an area of fine quartz grit of <200m^2 (Figure 9). This autumn-flowering *Conophytum* was discovered by Chris Rodgerson in 1994 and subsequently described by Steven Hammer in 1997 (Hammer, 1997). Also described at the same time by Hammer, *C. chrisocruxum* lies just 2km to the northeast of *C. chrisolum*. By contrast with *C. chrisolum*, *C. chrisocruxum* is readily caespitose and inhabits the shaded vertical cracks and fissures in large quartz blocks (Figure 10). The accompanying succulent flora of these two sites is similar to the ridge where *C. bachelorum* and *C. confusum* are found, although it is worth noting that *Tylecodon cordiformis* is endemic to the site of *C. chrisocruxum*.

All four populations of *Conophytum* inhabit quartz but the niche habitat differs. *C. chrisocruxum* and *C. bachelorum* are primarily found in vertical cracks and crevices in large boulders, the former almost exclusively so. The strong preference for a shaded habitat at higher elevation (typically south or southwest-facing steep cliffs) in *C. chrisocruxum* is not seen in the other three taxa, which are found in full sun to semi-shade. *C. bachelorum*, for example, spills over into small, sometimes open, flat patches of quartz rubble. By comparison the *C. chrisolum* and *C. confusum* primarily inhabit flat areas of quartz, notably the former which is exclusively found in densely packed, fine quartz grit. *C. confusum* is found scattered on the flats amongst smaller quartz boulders and pebbles, and only occasionally in cracks on larger quartz rocks.

Perhaps the most fascinating aspect of these endemics is that the two pairs of *Conophytum* taxa found on each hill exhibit temporal separation of flowering. *C. bachelorum* and *C. chrisocruxum* flower in spring, whereas *C. chrisolum* and the new taxon flower later in the year during the late summer or early autumn. There are unanswered questions as to why such large temporal separation of flowering should evolve in this way for these particular taxa when it is so uncommon within the genus. Spring flowering is very rare in *Conophytum* with fewer than 5% of taxa exhibiting such behaviour. There are no indications, for example, that the flower structures from the spring and autumn-flowering taxa differ so markedly that different pollinators may be involved, although this must be a possibility. Unfortunately there are very few recorded habitat observations of *Conophytum* pollinators that would allow us to better understand the influence of this. One of the few studies that did explore this identified pollen wasps as the main pollinator of day-flowering *Conophytum* species (Jürgens and Witt, 2014). *Conophytum* taxa that flower in the spring align themselves with the flowering period of a majority of succulent flora in Namaqualand.

Not only do *C. bachelorum* and *C. chrisocruxum* share a common flowering period, they possess pink petals. By contrast, the flower petals of *C. chrisolum* and the new taxon are magenta coloured with externally visually brilliant tubes. The flower structure (Figure 11) is similar to that of *C. obscurum* (an autumn-flowering species widespread in the area and found on both hills), and another localized endemic, *C. ectypum* ssp. *cruciatum*, which occurs a few kilometers northeast of *C. chrisocruxum* in very large numbers.

In terms of morphology, the four taxa considered here, namely *C. bachelorum*, *C. chrisolum*, *C. chrisocruxum* and the newly discovered species are clearly linked by similar and distinctive leaf epidermal characters in that they share a glabrous epidermis. In the newly discovered taxon the leaf epidermis is perfectly glabrous, completely lacking trichomes, papillae or other outgrowths of the epidermal cells. As seen in surface view, the epidermal cells are simple polygons and mostly hexagonal, with straight anticlinal walls. The outer periclinal wall is strongly convex, and contains abundant crystal sand, most likely calcium oxalate. By comparison to the three other taxa the surface of individual epidermal cells is somewhat more flattened in *C. bachelorum*, *C. chrisolum* and *C. chrisocruxum*. Stomata are associated with two subsidiary cells, also polygonal in outline with straight anticlinal walls. Within section Wettsteinia (to which we believe all four taxa belong), only one other species, *C. ricardianum*, lacks papillae or trichomes on its epidermal cells, and in general such a microscopically smooth leaf surface is quite unusual in the genus *Conophytum* (Opel, 2005). The form and number of subsidiary cells, as well as the distribution of crystal sand, in the epidermis of the new taxon is identical to what is seen in *C. bachelorum* and its relatives, although these character states are not as diagnostic, and do occur in other members of section Wettsteinia (Opel, 2005). It is also worth noting that the leaves of *C. confusum* are consistently several mm smaller in diameter than those of *C. bachelorum*.

So how is it best to rationalise this group of four, rare, point-endemics? One could simply consider these as two pairs of *Conophytum* with one from each pair growing in each location. These specific pairings [*C. chrisocruxum* - *C. bachelorum*] and [*C. chrisolum* - *C. confusum*] are best defined on the basis of differences in flowering time (spring v. autumn, respectively). This behaviour is extremely rare in the genus but there is one other example worth mentioning: *C. smorenskaduense* (flowering in late winter, inhabiting fine quartz) and *C. hermarium* (autumn flowering, inhabiting cracks in large quartz boulders) are separated by <5km on the farm Smorgenskadu just east of Springbok. Once again in this pairing we have a combination of morphologically similar plants with contrasting habitat niches (a point raised by De Boer in his original description of *C. smorenskaduense,* de Boer, 1968) coupled with temporal separation of flowering.

Whilst the taxa in the pairings proposed here share some similarities in habitat, growth form and flower colour these are not always consistent with an association simply based on flowering time. For example, *C. confusum* and *C. bachelorum* are closer to each other morphologically than the other two taxa: they both possess larger, finely spotted bodies that, uniquely, accumulate bronze-red pigments (presumably betalains) in full sun (Figure 12). This characteristic is much less evident in either *C. chrisolum* or *C. chrisocruxum*.

Description

C. confusum shares some affinities to three other *Conophytum* taxa, namely *C. chrisolum*, *C. chrisocruxum* and *C. bachelorum.* In particular all four taxa possess a glabrous epidermis and similarities in body shape (obconical) and outline (circular in section). *C. confusum is* geographically closest to *C. bachelorum* but is differentiated by possessing smaller bodies that are more inclined to (frugal) clustering, by the disjunct flowering time and differences in the colour of the corolla-tube: showy magenta vs. washed-out green. With *C. chrisolum* it shares both a similar flower structure and flowering time, together with a preference for growing in areas of flat, chipped quartz, but *C. confusum* is much larger and forms clusters, unlike *C. chrisolum* which remains solitary (only exceptionally dividing in old and well-fed age). The relationship between *C. confusum* and *C. chrisocruxum* is perhaps less obvious, with differences in clustering (the latter often forming large plants in habitat), flowering time, markings around the fissure and habitat (sun versus shade) serving to distinguish between the two taxa. Similarities in the structure and colouration of the flowers of *C. confusum* and *C. obscurum* also raise questions regarding their relationship. However, the epidermis of *C. confusum* (and that of *C. bachelorum, C. chrisocruxum* and *C. chrisolum*) is quite distinct from that of *C. obscurum*, which has a microscopically papillate leaf surface.

Whilst there are clear affinities between these taxa, their precise relationship to each other remains uncertain. Because of these uncertainties we have chosen not to define the new taxon as a subspecies of one of the related taxa but rather describe it at species level.

C. confusum A.J.Young, C.Rodgerson, S.A.Hammer & M.R.Opel subg. **Derenbergia** Section **Wettsteinia. Type** Adam Harrower (ADH) 4777 (National Botanical Gardens, Compton Herbarium, Kirstenbosh Cape Town. Date of collection: 8th September 2011; holotype)
Solitary or slowly branching; **Leaves** body obconical, apex flat or slightly depressed, circular in section, rich saturated green to deep maroon, glossy, densely but finely spotted, to 10 mm diameter, to 11 mm tall; **Flowers** appearing in early autumn, sepals pale tan (4), petals magenta becoming paler towards the centre with a magneta tube, few; **Fruit** pale tan, shallow, 4 locules, seeds pale brown

0.45 x 0.65 mm; **Ecology** in quartz gravel; **Distribution** Namaqualand, Northern Cape, S Africa, 2917AD.

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FIGURE LEGENDS

Figure 1. General location of the four *Conophytum* taxa discussed here in Namaqualand, Northern Cape, South Africa.

Figure 2. The quartz ridge that is home to both *C. confusum* (foreground) and *C. bachelorum* (beyond the ridge summit in the far distance).

Figure 3. The local habitat of *C. confusum*. Here growing typically in full sun amongst small quartz stones and yellow flowering clusters of *C. meyeri*.

Figure 4. Close up of *C. confusum* in habitat, shortly after flowering has finished showing the presence of recent flower remains (April 2008). Note that the perforated sheath is very distinctive in this taxon but is not in itself diagnostic.

Figure 5. A cluster of several plants of *C. confusum* growing with *C. meyeri* at the former's Type Locality.

Figure 6. *C. bachelorum* in habitat <2km west of the location of *C. confusum*.

Figure 7. A solitary individual of *C. bachelorum* in flower in habitat. A majority of plants observed in habitat were single bodied.

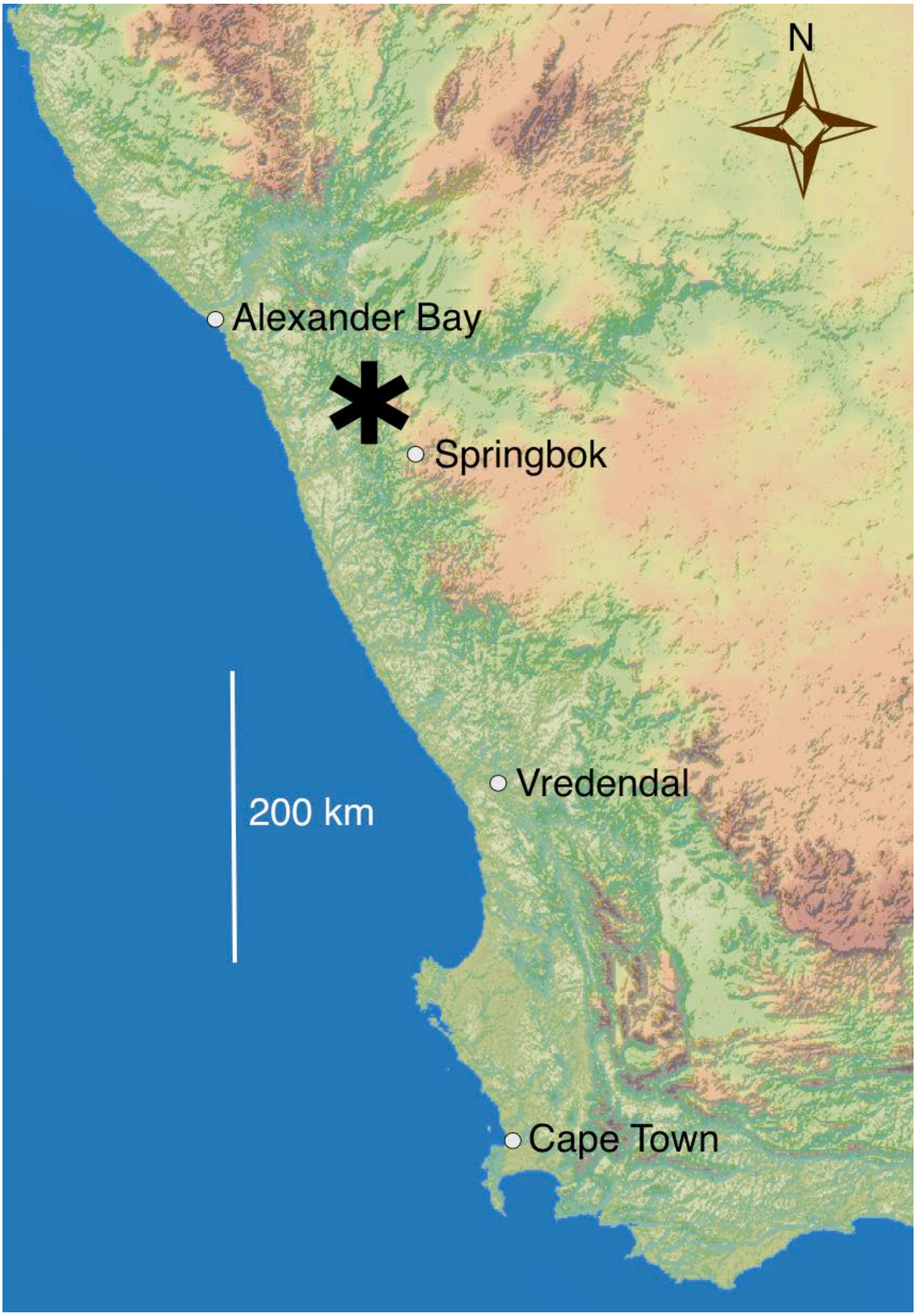
Figure 8. *Adromischus marianiae "herrei"* growing alongside *C. bachelorum. This Adromischus* is also found with *C. confusum* in the shade of bushes and in rock fissures. A similar form of *A. marianiae "herrei"* is found close to *C. chrisocruxum*.

Figure 9. *Several individual plants of C. chrisolum* in the fine quartz grit that defines their habitat.

Figure 10. *C. chrisocruxum* is typically found in large clusters growing in the shade provided by cracks and fissures in large quartz boulders.

Figure 11. The late summer / early autumn (April-May in habitat) flower of *C. confusum* showing a clear resemblance to the flower of *C. obscurum* (c.f. photographs on page 196 of Hammer, 2002).

Figure 12. A de-sheathed body of *C. bachelorum* showing the distinctive finely spotted epidermis and bronze-red pigmentation towards the edge of the leaf. The epidermis of *C. confusum* is similarly spotted and can also redden in full sun (a characteristic less evident in both *C. chrisolum* and *C. chrisocruxum*). Such colouration can intensify and extend over the entire exposed surface prior to the plants resting in the spring.



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