

Land of blooming pebbles: flowers and their pollinators in the Knersvlakte

Mike Struck



Figure 1. "El Dorado" of peculiar growth forms: The bizarre *Dactyloopsis digitata* and flowering *Cephalophyllum spissum* on a cool winter day.

Driving along the National Road between Vanrhynsdorp and Bitterfontein, the traveller encounters a barren landscape of rolling hills which seem to support only scattered patches of dwarf shrubby vegetation. The dazzling cover of white quartz pebbles and the sweeping winds add to the bleakness of this featureless region which is called the Knersvlakte.

Mimics of their surroundings

"Moet nie op vetplante trap nie – Do not step on succulents" – the sign-board cautions visitors to stick to the "Vetplantevoetslaanpad" (Succulent trail) which leads through a farm camp at the banks of the Soutrivier. While one is still wondering about the significance of this warning, unexpectedly some stones of a different kind leap to the eye: camouflaged by their silvery skin, the cryptic fat-leaved argyrodemas assume shape among the pebbles, opophytums pop up like miniature cauliflowers and a little further the bizarre *Dactyloopsis digitata* raise their "vinger-en-duime" (fingers-and-thumbs). This is indeed a "dorado" of peculiar growth forms, some of which evolved convergently in unrelated plant groups (Figures 1 and 2). The Knersvlakte is one of the major centres of diversity, particularly for leaf-succulents, and provides

habitats for many endemics. Known as the "Vanrhynsdorp Centre" (Nordenstam 1969), the Knersvlakte basin encompasses a flora of some 600 to 800 species of which about 20% are endemic to this region (A. le Roux, CDNEC and C. Hilton-Taylor, NBI, pers. comm.)

Harsh environment

The Knersvlakte is situated in a low-lying basin of about 300 m above sea level, which opens towards the Sandveld in the west. Towards the south and east it is framed by the steep Bokkeveld and Mat-sikamma Mountains (Figure 4); to the north it borders on the foothills of the Namaqualand Rocky Hills. Rainfall is extremely erratic in space and time: at Vanrhynsdorp weather station, the average annual rainfall is 150,5 mm (Weather Bureau 1986) which is mainly received during the winter months. However, at the farm Quaggaskop, just some 25 km further north, rainfall ranges between 62 and 75 mm per year and might rarely amount to up to 100 mm (B. Wiese, pers. comm.) Coastal fog regularly penetrates deeply into the Knersvlakte basin, particularly along the valley of the Soutrivier, which adds some precipitation and administers a cooling effect. The underlying rock consists mainly of phyllite schist streaked with more or less mighty

quartz veins. Gradients of decreasing soil depth and soil moisture storage capacity – together with small scale fluctuations in the soil chemistry – produce a distinct pattern in the distribution and composition of the vegetation (Jürgens 1986, Schmiedel 1994). Characteristically, the vegetation of the quartz hills is composed of "monodominant units" – i.e. a patchwork of almost pure stands of single species, such as argyrodemas, opophytums or dactyloopsis which are supplemented by a choice of a few other taxa (compare Figures 1 and 7).

Duck and hide

Most of the compact succulents become invisible during the dry season by shrinking close to or even below the quartz pebbles. These ground-hugging plants protect themselves from overheating and detection by means of a thick silvery or whitish xeromorphic epidermis or – in the soft-skinned species – by the withered leaves of the previous season which are retained to cover the vital water-storing young leaves like a second skin (Figure 5). With the onset of the rainy season the plants literally burst into active growth again. Breaking through their protective wrappings, the young leaves mature to full size. In many species only a single leaf pair per plant or branchlet is

initiated – the absolute minimum necessary to reproduce every year (Figure 6). Other species shed their leaves and sometimes even their branches to survive the adverse season underground, reappearing miraculously with the onset of the cool season. Where the soil is too shallow to sustain even these never-say-die fellows, leaf-succulent annuals *Opophytum fastigiatum* and *Mesembryanthemum nodiflorum* may abound in moist years.

Blooming season

As in other parts of the southern African arid winter rainfall region (Le Roux et al. 1989; Struck 1992, 1994a) spring is the main flowering season. However, the cryptic argyrodermas present their large, peculiar “cavity flowers” already during the autumnal months. If conditions are right, the barren quartz hills become tinged with pink or yellow patches – colourful heralds of more to come (Figure 7). In contrast, the bizarre *Dactyloopsis digitata* produce their tufted white flowers in early summer at a time when most plants have retired for the period of rest (see Figure 14). Later in summer all life seems to come to a halt. But even in the shimmering heat of a hot February day the tiny *Tylecodon pygmaeus* present their greenish flower cups (Figure 8).

As can be expected, flowering is greatly moulded by the prevailing weather conditions. The vigour and to some extent duration of flowering is subject to the



Figure 2. Thumbs up! *Bulbine diphylla* shares habit and habitat with *Dactyloopsis digitata*.

amount of precipitation received before and during the blooming season (Struck 1994a). The result of high or low moisture availability is most easily seen in the flowering performance of the annual flora. Nevertheless, rainfall is not the overriding environmental factor to control the timing of flowering: although the onset of the blooming season varies from year to year, the sequence of flowering phenologies of the co-occurring species remains largely unchanged (see Figure 2). This is because the timing of the blooming – as

part of the yearly cycle of seasonal activity and dormancy – is not linked to the highly erratic rainfall events, but rather to more predictable triggers mediated through temperature changes (Van Rooyen et al. 1991, Struck 1994a).

Floral design and function

As is characteristic throughout Namaqualand, the great majority of plants show entomophilous pollination syndromes, i.e. the transfer of pollen involves a delivery service by insects. Large to small, expanded, brightly coloured flowers and asteraceous capitula abound, which offer copious amounts of pollen and (usually little) nectar within easy reach to a wide range of (short-tongued) insects (Figure 9). Nevertheless, these and other flowers are not foraged at random. Slight differences in shape and colour allow insects to recognise their favourite host plants (Figures 10 and 11). On the other hand, subtle differences in the arrangement and size of the petals, stamens and stigmas determine which part of the insect body will actually become dusted to transfer pollen onto the stigmas of the next conspecific flower. All this minimises the loss of pollen. Moreover, many flower-visiting insects, particularly beetles, frequently use flowers not only as a food source but also as a mating place (“rendez-vous” pollination). In this regard, the argyrodermas appear specifically well equipped: their flowers possess a fairly

	JAN	FEB	MAR	APRIL	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC
<i>Tylecodon pygmaeus</i>		■										
<i>Conophytum minutum</i> var. <i>minutum</i>				■	■							
<i>Conophytum subfenestratum</i>				■	■							
<i>Argyroderma delaetii</i>				■	■							
<i>Ruschia solida</i>					■	■						
<i>Argyroderma pearsonii</i>					■	■						
<i>Piранthus punctatus</i>					■	■						
<i>Oxalis</i> sp.					■	■						
<i>Cephalophyllum spissum</i>						■	■	■				
<i>Argyroderma fissum</i>						■	■	■				
<i>Drosanthemum diversifolium</i>							■	■	■			
<i>Oophytum nanum</i>							■	■	■			
<i>Crassula columnaris</i>							■	■	■			
<i>Phyllobolus abbreviatus</i>							■	■	■			
<i>Pteronia heterocarpa</i>							■	■	■			
<i>Euphorbia exilis</i>							■	■	■			
<i>Aridaria brevicarpa</i> , <i>A. noctiflora</i> , <i>A. serotina</i>							■	■	■			
<i>Mesembryanthemum nodiflorum</i>							■	■	■			
<i>Anacampseros retusa</i>								■	■			
<i>Dactyloopsis digitata</i>										■	■	■
<i>Zygophyllum cordifolium</i> *					■	■	■	■	■			
<i>Zygophyllum teretifolium</i> *					■	■	■	■	■			
<i>Othonna protecta</i> *					■	■	■	■	■			
<i>Othonna intermedia</i> *							■	■	■			

Figure 3. Generalised flowering phenologies of selected species from the central Knersvlakte. In response to the prevailing climatic conditions, the onset of the blooming season is subject to considerable variation, nevertheless, the flowering sequence remains consistent between the years.

*Very variable in response to moisture availability.

spacious cavity ("hypanthium"). The stamens are borne around the upper rim and bend down into the recess to form a ruff-like entrance to the cavity. The short stigmas are fused into a disk and spread onto the bottom of the flower in a position apparently invulnerable to the chewing mouthparts of visiting beetles which have to enter the cavity to feed on pollen (Figure 12).

By contrast, the trumpet-shaped flowers of the "kriedoring" (*Lycium cinereum*), the yellow "bells" of the "broodbos" (*Hermannia cuneifolia*) or the tubular flowers of conophytums are too narrow to be entered (Figure 13). These flowers which offer nectar as the principal reward are usually exploited by bees and butterflies with long mouthparts. In *Dactylopsis* short-tongued insects are excluded by means of numerous slender and stiff petals which conceal the nectaries and anthers (Figure 14).

As has been observed in other parts of Namaqualand (Struck 1992, 1994b) most of the diurnal flowers open between 10 and 11 a.m. and close again between 5 and 6 p.m. unless delayed or brought forward by overcast skies, fog or rain. By contrast, the shrubby *Aridaria serotina* and *A. noctiflora* var. *noctiflora* are truly night-flowering, showing a conspicuous overlap in their flowering times (Gerbaulet in prep.). Both species share their habitat with yet another "donkiebos", *A. brevicarpa* which, however, is strictly day-flowering. All three "donkiebossies" are extremely similar in growth form and habit and even produce almost identical whitish, bunchy and strongly scented flowers. It seems peculiar that the nocturnal flowers exude almost the same perfume reminiscent of artificially flavoured sweets, while the odour of the diurnal blossoms is quite distinct. Nevertheless, these taxa do not appear to lose their genetic integrity (Gerbaulet in prep.), although they share the same habitat and blooming season.

The most sophisticated floral syndrome encountered during the present study is found in the "trap flower" of *Puranthus punctatus* (Figure 15). In contrast to most stapeliad "carrion flowers", this species emits a honey-like floral fragrance. The pollinators are presumably flesh flies (Sarcophagidae) (Meve 1994, Meve & Liede 1994).

Flower visitors

Honey bees and butterflies are widely perceived as the most important, if not the only, groups of flower-visiting ("anthophilous") insects or pollinators. However, plant communities of the arid parts of southern Africa harbour a much wider



Figure 4. The southeastern corrie of the Knersvlakte basin viewed from top of Vaurhyns Pass.

spectrum of anthophilous insects, of which solitary bees, masarine wasps, bee flies and certain beetles figure as the most diverse and abundant groups (e.g. Gess 1981; Gess & Gess 1989, 1993; Struck 1994b).

Similar conclusions can be drawn from preliminary field observations conducted in the central Knersvlakte: a wide range of bees (14 solitary bee species plus the social honey bee), masarine wasps (8 species), flies (7 species), beetles (13 species) and occasionally butterflies (3 species) were encountered as flower visitors on 30 host plant species (see Appendix). Most insect taxa showed a distinct period of activity once the temperature had risen after the winter chill.

In terms of diversity and abundance, bees, masarine wasps and bee flies (Bombyliidae) appear to be most important as pollinators (see Figures 14, 16 and 17). All three groups depend on nectar as a direct energy source for adult flight. In addition, bees and masarine wasps collect pollen and nectar for larval provision (Neff & Simpson 1993, Gess & Gess 1989), while female bee flies frequently ingest pollen through their probosces as a protein source for egg maturation (Deyrup 1988 and references cited therein). This high degree of dependence on a floral diet makes all three groups highly "motivated" flower visitors. Moreover, they exhibit a very similar visitation behaviour and are therefore often classified into the single anthecological group of "Melittoids" (bee-like pollinators), as opposed to the other pollinator classes, like butterflies or beetles (Vogel 1954, Whitehead et al. 1987 [without mentioning the Masarinae], Struck 1994c). However,

while bee flies often switched between species of flowers during a foraging bout, bees and masarine wasps generally exhibited a high degree of flower constancy.

Butterflies occurred in a highly erratic fashion, both in space and time. These insects also rely on nectar as a primary energy source, but most species did not show particular floral preferences. Nevertheless, a few plant species appear to be dependent on butterflies as their primary pollinator, e.g. *Conophytum* spp.). Flower-visiting beetles, most prominently "monkey beetles" (Hopliini), melyrid and meloid beetles are all feeding on floral parts, but are also "rendez-vous" attracted (see above). These small to medium-sized insects were encountered on a wide variety of flowers, but mostly on large, open asteraceous capitula or mesemb flowers (e.g. *Argyrodema* and *Cephalophyllum* spp.) in which they aggregated in considerable numbers (Figure 9). Most insect species are not specialised to exploit a particular host plant species (see also Struck 1994c), with the notable exception of *Fidelia paradoxus* bees (Figure 16 bottom) which are recorded as specialist visitors (and pollinators) of *Oxyphytum fastigiatum* in the study area (Whitehead 1984).

Plant-pollinator mutualisms

As mentioned above, the flowers presented are not foraged at random, but are rather visited according to the structural and behavioral abilities of the various anthophilous insects. Thus, one can observe that certain flowers are most attractive to bees, while others are primarily visited by butterflies or moths. "Bee

flowers" or "butterfly flowers" and other "floral syndromes" are characterised by their perianth shape, floral colour and scent, many of which evolved independently and repeatedly in unrelated plant groups. However, these floral syndromes are by no means exclusive. In fact, most flowers may effectively be pollinated by members of various pollinator classes. Hence, details on pollination syndromes (see Table 1) as given below merely indicate the primary pollinator class, based on the available field data.

Of the 36 plant species sampled for flower-visiting insects (see appendix), 11 species are pollinated by members of different pollinator classes: 7 of these species present unspecialised flowers which are open to a wide range of short-tongued insects (allophilily). Nineteen species appear to be primarily melittophilous with bees, bee flies or masarine wasps as the major pollinators. Fruitflies and hoverflies were exclusively associated with *Euphorbia exilis* (myiophily). By contrast, the flowers of *Conophytum minutum* are specialised to visiting butterflies (psychophily, Liede et al. 1991). As mentioned above, the stapeliad *Piaranthus punctatus* appears to be pollinated by sarcophagid flies (sapromyophily) (Meve 1994, Meve & Liede 1994) and two *Aridaria* species are most probably moth pollinated (phalaenophily). Two species received too little insect visitation to be assigned to a particular pollination syndrome.

While in most plant species fairly broad levels of mutualisms are involved, 9 species are assumed to be oligophilic, i.e. specialised to one or a few related insect taxa. These include the mellitophilous *Anacampteros retusa*, *Dactylopsis digitata*, *Hermannia cuneifolia*, *Lycium cinereum*, *Phyllobolus abbreviatus*, *Sarcocaulon cruscicaude* and *Tylecodon pygmaeus*, the sphingophilous *Conophytum minutum* and the sapromyophilous *Piaranthus punctatus*.

Flower display – the enigma of the mass flowering

The blooming season welcomes visitors – of both the human and insect kind – with a most colourful mass display of pink, yellow, orange or copper flowers. This display is the result of apparently stiff competition to attract pollinators (Cohen & Shmida 1993) – for the abundance of flower-visiting insects is remarkably low. Such a paradoxical situation has also been recorded from other arid areas (Linsley 1958, Moldenke 1976, Struck 1994c). Moreover, inclemencies of the weather frequently interfere with insect activities: fog or cloudy weather with low temperatures and rain occur particularly during the spring flowering season, which is also the principal flight period of the anthophilous ("flower loving") insect fauna. Strong winds are common throughout the year and reduce the times of insect activity (and the chances for pollination) even further. Thus, in order to achieve sufficient pollination, the plant species exhibit a variety of adaptations. The following pointers refer specifically to the perennial plants.

– (1) Flowering occurs in a more or less fixed sequence at a given locality (see Figure 3). This allows the insect pollinators to emerge from diapause (temporary pause in insect development during the hot season) accordingly. The co-ordination in timing of flowering and insect activity is possible, since both are ultimately triggered by the same environmental cues (see Struck 1994a,c). Although the exact timing of flowering and insect activity is subject to a considerable yearly fluctuation, both were generally found to be well in tune.

– (2) The onset of flowering is extremely fine-tuned within a given plant population, although the exact timing may vary



Figure 5. Old skin bags and a pachyderm – *Conophytum nanum* and *Argyroderma delaceti* during their summer rest.

at different localities nearby. In most species anthesis is highly synchronised within and between individual plants, which results in a "big bang" type of flowering. In certain mesemb species, a perfect synchronisation of anthesis is facilitated by adaptations in inflorescence structure (Ihlenfeldt 1989): inflorescences are reduced to single terminal flowers which are produced on a number of lateral shoots (e.g. in *Conophytum*). Moreover, the visual attraction of the mass flowering species is even more enhanced by their patchy distribution (see above).

– (3) Cryptic mimics of the genera *Argyroderma* and *Conophytum* exemplify the operation of sexual selection: being vegetatively well camouflaged and inconspicuous turns out to be disadvantageous for the attraction of pollinators. This is overcome by especially large and showy flowers (which in turn may render the plants liable to some predation), and by a high synchronisation of anthesis in a given population.

– (4) The species co-occurring in a particular habitat diversify in the principal floral reward and to a lesser extent in pollination syndromes. Generally, pollen-rewarding species (e.g. most ruschioid mesembs) tend to attract a wide range of insect visitors, and levels of mutualism are quite broad. On the other hand, all species classified as oligophilous (see above) offer primarily nectar. These species usually exhibit a scattered distribution (see below). *Opophytum fastigiatum* offers both, pollen and nectar, in ample quantities.

– (5) Beside the mass-flowering species there are a number of taxa with a scattered occurrence and low numbers of

allophilic flowers	flowers that lack morphological adaptations to direct pollinators and can be used by short-tongued insects
mellitophily	floral syndrome involving pollination by bees
myiophily	floral syndrome involving pollination by flies
phalaenophily	floral syndrome involving pollination by moths
psychophily	floral syndrome involving pollination by butterflies
sapromyophily	floral syndrome involving pollination by carrion- and dung-flies
oligophilic	pollinated by a few related taxa of flower visitors
polyphilic	pollinated by a variety of different taxa of flower visitors
flower constancy	a tendency of flower visitors to visit a single species of flower during a foraging bout

Table 1. Glossary of terms relating to flower-pollinator mutualisms (compiled from Kearns & Inouye (1993)).



Figure 6. Miraculous transformation – *Conophytum subfenestratum* almost vanishing during summer (left) and in flower during autumn (right).



Figure 8. Blooming bonsai – *Tyloscladon pygmaeus* flowering in February after the leaves are shed.



Figure 7. Flowering pebbles – *Argemone parsonii* in full bloom in early winter.



Figure 10. A typical *Ruschia* flower with a female *Patellapis* bee harvesting pollen from the "staminodal cone".



Figure 9. Everybody is welcome! Flower-visiting dasytine beetles and a halictid bee (centre) on *Cephalophyllum spissum*.



Figure 11. Small is beautiful! *Oxyphium nanum* visited by masarine wasps of the genus *Quartacoides* and dasytine beetle.



Figure 12. Designed for clumsy pollinators – The peculiar floral cavities of *Argyroderma parsoni* with *Prolytta semilunata* (left) and *A. fissum* (right; in longitudinal section).

flowers which remain relatively inconspicuous, at least to the human eye. Examples include *Phyllobolus abbreviatus* and *Tylecodon pygmaeus*. An extreme case is found in the obscure *Anacamptseras retusa* in which individual flowers last for but a few hours (cf. Gerbault 1992)! All these species provide ample nectar as the principal reward for their insect pollinators. Species of this category were observed to receive rare but regular visits by specialist pollinators (oligophilous pollination syndrome).

Due to the yearly fluctuations in the prevailing seasonal weather conditions, the vigour of a species' blooming may be promoted in one year and retarded in another (Struck 1992, 1994a). This will result in correspondingly low or high pollinator visitation rates, since plant species tend to become more attractive to their floral visitors the more flowers they can offer (Thomson 1981, see Struck 1994c). It is important to note that the plant species differ in their response towards the yearly climatic variables. As a result, the reproductive success of the co-occurring species differs as well in a particular blooming season; in other words a "good" year in terms of flowering and seed set for species A is not necessarily as good for species B.

On the other hand, most insect species are not specialised to exploit a particular host plant species (see above). The decision regarding which of the potentially suitable host plants to forage probably follows the law of "supply and demand" (of course within the borders of suitable flower species). Once a decision has been taken, high degrees of floral constancy are usually maintained (Struck 1992, 1994c). As a result, the insect visitors are

able to switch to the most suitable and rewarding host plants in a given blooming season.

With regard to the interspecific competition to attract pollinators it can be concluded that the plant species take advantage of the unpredictability of the environmental parameters (Fagerström & Agren 1980, Struck 1994d). Since the co-occurring species vary in their flowering success (and thus in pollination success) from year to year, interspecific competition for pollinator visitation can be expected to be lowered in the long run. This in turn will contribute to the maintenance of the high species diversity of the flora native to the Knersvlakte.



Figure 14. Reward concealed – *Dactyloctenium aegyptium* visited by masarine wasps of the genus *Quartinioides*, members of this genus are equipped with exceptionally long tongues.



Figure 13. Specialised on long-proboscid flower visitors – A specimen of *Conophytum minutum* var. *minutum* prepares for the flowering season.

Methods and Acknowledgements

The field data for the present account were accumulated during 14 visits to the central Knersvlakte conducted from July 1992 to April 1994. The principal study site was situated on the farm Quaggaskop some 25 km north of Vanrhynsdorp. Flowering phenologies were monitored for 24 species (see Figure 2) and 36 species out of 24 genera and 11 families were sampled for insect visitors (see Appendix). In total about 120 hours were spent with field observations.

Special thanks are due to Mr Buys Wiese, Vanrhynsdorp, for sharing his intimate knowledge of the Knersvlakte and for granting permission to explore flowers and insects on his property. To the staff of the Cape Department of Nature Conservation my sincere thanks for collecting permits. I am indebted to C.D. Eardley (SANParks), S. Endrödy-Younga (TRVM), F.W. Gess (AMGS), D.J. Greathead (Centre for Population Studies, Ascot), T. Griswold (USDA) and V. Whitehead (SAMC) for identifying insect vouchers. Ute Schmiedel (University of Hamburg) kindly provided hitherto unpublished data on the ecology of habitats and the structure of the vegetation of the central Knersvlakte; A. le Roux (CDNEC) and C. Hilton-Taylor (NBI) kindly contributed educated guesses on plant diversity and the proportion of endemics, respectively; M. Gerbault and S. Hammer provided useful comments on the manuscript. The research was supported by the FRD and the Merensky Foundation.