EDITORIAL

This special part of *Curtis's Botanical Magazine* concentrates on the iridescent spots found on the flowers of many plants in South Africa – particularly in the Cape. These have long been the subject of comment by botanists, but were noticed especially by Rudolph Marloth and many examples were described in volume 4 of his *The Flora of South Africa* published in 1915.

Here Peter Goldblatt and John Manning, well known for their monographs of South African Iridaceae and *Checklist of the Cape Flora*, present an overview of pollination by monkey or hopliine beetles and the different families and genera in which iridescent spots or patches have evolved.

Nine species with iridescent spots are illustrated with photographs and with paintings by Georita Harriott, of specimens grown in the University Botanic Garden, Cambridge. They include Iridaceae, especially several *Moraea* species, Hypoxidaceae and Compositae. One of the most striking is the annual beetle daisy *Gorteria diffusa* where the beetle-like spots are produced – apparently randomly – on the ray florets. *Gorteria* is not pollinated by hopliine beetles but by a small bee-fly (*Megapalpus capensis*) which sees the spots as potential mates, resting on a plain flower. This was reported by Allan Ellis and S.D. Johnson in 2010 (see page 34~~7~~) and is the first example of pollination by sexual deception known in flowers other than orchids.

The structure and development of those spots has been studied recently by Allan Ellis and a group in the Cambridge University Botany School, using a scanning electron microscope to see the shape and structure of the cells, and some results of this research are described and illustrated here.

As a contrast we have included *Massonia bifolia* (Jacq.) Manning & Goldblatt, which flowered at Kew last winter. It is more commonly known as *Whiteheadia latifolia* Harvey, but was originally described as a *Eucomis*. This South African bulb, in the family Hyacinthaceae, has an upright inflorescence of small flowers with broad fleshy cup-like bracts which hold the sticky nectar for the pollinators, usually the Namaqua Rock Mouse, but sometimes the Cape Rock Elephant-shrew.

Martyn Rix

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HOPLIINE BEETLES (SCARABAEIDAE: RUTELINAE: HOPLIINI), SPECIALIZED POLLINATORS OF THE SOUTHERN AFRICAN FLORA

Peter Goldblatt and John C. Manning

Introduction

One of several specialized pollination systems identified in southern Africa, hopliine beetle pollination was barely known until 1990 when research on pollination studies in the southern African flora began to receive serious scientific attention. Although almost worldwide in distribution, hopliine beetles (Scarabaeidae: Rutelinae: Hopliini), have their centre of diversity in southern Africa, where some 1040 species are recorded, 98% of them endemic to the subcontinent (Colville, 2009; Ahrens *et al.*, 2011). Known locally as monkey beetles from their densely hairy bodies and active behaviour, the subtribe Hopliini includes many conspicuous, large, sometimes colourful insects that actively visit flowers during the day, particularly in the winter-rainfall zone in the southwestern part of the subcontinent, where over 200 species have been recorded.

The first reference to hopliine beetles as pollinators of the southern African flora is by Scott Elliot (1891), and later Peringuey (1902), who remarked on the frequency with which beetles visited southern African wildflowers, commented further that hopliines in particular departed from flowers covered with pollen, and that 'on a bright day in the spring (August to October) no flower is without a tenant'. He maintained that few insects were better adapted for flower pollination than the hairy hopliines of the genera *Anisonyx*, *Lepithrix*, and *Peritrichia.* Marloth (1915) subsequently drew attention to the similarity between the dark green markings of flowers of *Spiloxene capensis* and visiting *Anisonyx* beetles and noted that beetles preferentially visited *Spiloxene* flowers with dark centres. Curiously, Vogel (1954) in his mammoth review of pollination systems in southern Africa did not cite Peringuey, and although he noted that some scarab genera were pollen- and flower-eaters, he made few overt references to beetle pollination. The subject remained virtually dormant for the next 35 years, and Whitehead *et al.* (1987) in their review of insect pollination systems in the Cape Flora (part of the

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winter-rainfall climate zone of southern Africa) made no mention of hopliines as important flower visitors. More recently, Johnson (1992) briefly mentioned hopliine beetles as visitors to Asteraceae and Bruniaceae, and also noted that they often visited red flowers.

Subsequent studies have now made it clear that hopliine scarab beetles constitute an important group of pollinators in southern Africa and that certain suites of floral characters are associated with hopliine pollination. In their touchstone paper, Picker & Midgley (1996) listed some 25 species of plants in the southern African flora as putatively pollinated by hopliines. These included both monocots and dicots representing some 10 families. More importantly, Picker & Midgley recognized two distinct systems of hopliine pollination, based on differences in beetle hairiness, flower colour preferences, and kind of plants visited. Embedding behaviour was confined to large inflorescences of Asteraceae and flowers of Aizoaceae: Mesembryanthemoideae, and beetles that showed this behaviour tended to have smooth bodies, which they buried in the flowers, in Asteraceae among the disc florets. This activity resulted in damage to flowers as a result of consumption of pollen, perianth parts and even ovaries. Flowers in this group are pollination generalists, receiving pollinating visits from a range of other insects as well. A second behaviour, involving non-embedding, usually densely hairy species of the genera *Anisonyx* and *Peritrichia,* seldom resulted in damage to flowers. Picker & Midgley (1996) deemed hopliines to be one of the important pollinator guilds for the southern Africa flora, and also demonstrated an unusual preference (among insects) for red flowers, and a low preference for blue or white flowers.

In a later paper describing the foraging behaviour of hopliine beetles, Goldblatt & Manning (1996) concluded that the genera *Anisonyx* and *Peritrichia* (as *Lepithrix*) were most likely the dominant (or sole) pollinators of two species of *Drosera* (Droseraceae) and one species each of *Aristea* and *Moraea* (Iridaceae) (Figs 1, 2). They also suggested that species of hopliines were likely to be the pollinators of many more species of Iridaceae in genera such as *Romulea*, *Sparaxis*, and *Tritonia*, as well as *Aristea* and *Moraea*. Two important studies by Steiner (1998a, 1998b) showed the significance of hopliine pollination in a species of Orchidaceae, and in the so-called peacock moraeas,

Fig. 1. Black *Anisonyx ursus*, the same colour as the outer tepals of *Aristea lugens*. Fig. 2. *Drosera cistiflora*, the light purple flowers have a dark centre, and a pair of *Anisonyx ursus* using the flower as a platform for assembly.

Moraea villosa and its close allies, as well as in *Sparaxis* and genera of Asteraceae including *Arctotis*.

Goldblatt *et al.* (1998) provided the first extensive study of hopliine pollination in southern Africa, showing that members of several plant families, both monocots and dicots, were effectively pollinated by hopliines and that these species shared certain characteristics. These included a radially symmetric flower, a bowl- or salver-shaped perianth or corolla, bright floral pigmentation with relatively large, sharply contrasting markings, and usually an absence of scent and nectar. To this we should add also compact, sturdy inflorescences, epitomized by the large capitula of many Asteraceae.

It is now also widely understood that adult hopliines use flowers as platforms for assembly, mate selection, competitive behaviour and copulation. The ephemeral adult hopliines emerge in late winter or spring when their host flowers come into bloom and live for a few weeks, mostly in association with flowers. Adults of some genera also consume floral parts and/or pollen and some hopliine-pollinated species, notably in *Aristea,* may compensate for pollen loss by possession of unusually large anthers compared with allied species.

Markings on hopliine-pollinated flowers are now considered to be 'beetle marks' (Goldblatt *et al.*, 1998; Van Kleunen *et al.*, 2007) that function in attracting potential pollinators. An early study, using model flowers of different colours and with or without markings, showed little preference to hopliine visitors (Johnson & Midgley, 2001), thus questioning the importance of beetle marks but a later study in a different area by Nänni and colleagues (Van Kleunen *et al.*, 2007) demonstrated an unequivocal preference by the local beetle fauna for model flowers with darkened centres or dark spots. Significantly more hopliines visited model flowers with spots or dark centres compared with unmarked ones.

Beetle diversity, physical parameters and behaviour

Hopliine beetles range in length from 6 to 14 mm. Body hairiness varies among genera and species, with *Anisonyx* having the densest and longest hairs. Among the smallest beetles are *Heterochelus arthriticus* and *Lepithrix stigma* (captured on *Romulea sabulosa*); among the largest are *Anisonyx ursus*. As many as five beetle species have been recorded on some species. Less than half (40%) of the plant species pollinated by hopliines were consistently visited by just one species of beetle. The life history of hopliine beetles has not been studied in any detail but females are assumed to lay eggs on the ground and larvae are subterranean. Emergence of adults coincides with the peak flowering season for the flora.

Hopliine beetles are most commonly seen on warm days in late winter and spring when ambient temperatures are above 18°C. Individual beetles have been observed in flight as early as 09.30 hours and as late as 16.00 hours, but peak activity on flowers is usually between 11.00 and 15.00 hours. Hopliine beetles fly readily but over relatively short distances. Beetle populations appeared to be most dense on inflorescences of Asteraceae and on the larger flowers of Aizoaceae: Mesembryanthemoideae. In contrast, beetles captured on other flowers rarely occurred in groups of more than two or three per flower. In these flowers, beetles were most often seen either foraging for pollen directly on anthers or pushing their heads into the flower centre, leaving the posterior portion of their abdomens prominently displayed. Since the anthers are usually positioned close to the centre of the flower and above the 'beetle marks' on the perianth, foraging beetles are usually observed positioned directly on the beetle marks.

When more than one beetle of the same species is present on a flower the insects often display intraspecific competitive behaviour, and one of the beetles is driven off as a result. The beetles also use the flowers as sites for mate selection and copulation. Compared to other animal pollinators, beetle visits to flowers last a relatively long time, at least several minutes, or more when mating or evidently at rest. Beetles also move to other flowers of the same species and to flowers of different species. Hopliine contact with stigmas occurred in one of two ways depending on the length and position of the style. In *Aristea* spp. and *Drosera cistiflora* and *D. pauciflora* (Figs 1, 2) the style or stigma is deflexed to lie parallel to, and above, the perianth surface. The stigmatic areas are thus distant from the center of the flower. In the second, more common, case the style is short and the stigma barely protrudes beyond the floral tube or cup. The hopliines then contact the stigma ventrally while crawling over it or dorsally when climbing into the floral cup. The colour of pollen of hopliine pollinated flowers is often so distinctive and contrasts so sharply with that of the beetles and the stigmas that pollen is easily visible clinging to the bodies of beetles and on the stigmas after the beetles have departed. The prominent dark outer tepal marks in some species of *Moraea* encourage the insects to move into the center of the flower directly under the style branches, where they are in a position to contact both pollen and stigmas.

THE HOPLIINE POLLINATION GUILD[1]

Prominent among the plant families with taxa adapted to visitation by hopliine beetles are Asteraceae and Aizoaceae: Mesembryanthemoideae, particularly among beetle species that show embedding behaviour. The family most prominently associated with non-embedding hopliines is Iridaceae, one of the largest families in southern Africa winter-rainfall flora (Goldblatt & Manning, 2000), where hopliine diversity is particularly high. Large, radiate-flowered Asteraceae have inflorescences preadapted as sites of assembly for

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[1] Authorities for plant species are found in Cape Plants, (Goldblatt & Manning, 2000) and are not given here.

Fig. 3. A flower head of *Ursinia anthemoides* with copulating *Pachycnema crassipes* pair. Fig. 4. *Sparaxis tricolor* and the dark brown *Anisocheilus inornatus*, the upper part of the thorax liberally covered with pollen grains.

beetles, providing a large, stable platform. One specialization that promotes hopliine activity is a dark disc or dark markings at the base of brightly coloured ray florets. Such inflorescences are common is several genera, notably several genera of Arctotideae (*Arctotheca*, *Arctotis* and *Gazania*) plus *Ursinia* (Anthemideae) (Fig. 3), and hopliine visitors have been recorded in all four genera (Goldblatt *et al.*, 1998). Although relatively few genera of Asteraceae have been implicated in hopliine pollination, it is undoubtedly present in several more. Significantly, dark markings on flowers, even those that seemingly represent beetles, do not always signal hopliine pollination, and the dark markings on the ray florets of *Gorteria diffusa* serve to attract the bee-fly, *Megapalpus nitidus* (Bombylidae), the only known pollinator (Johnson & Midgley, 1997).

Iridaceae, particularly diverse in southern Africa, presents several examples of different adaptations to hopliine pollination. The largest subfamily Crocoideae comprises mostly species with bilaterally symmetric, usually bilabiate flowers with the lower tepals provided with nectar guides, and a variously developed perianth tube offering nectar to insect visitors with elongate mouthparts. Such flowers are unsuitable for hopliine activity but hopliine type flowers have nevertheless evolved in several southern African genera through progressive loss of bilateral symmetry and the development of a radially symmetric perianth, accompanied by shortening of the perianth tube and reduction in nectar secretion. Flowers of three species of *Tritonia* plus *Sparaxis grandiflora* have bowl-shaped flowers with a radially symmetric perianth but maintain asymmetry in the unilateral orientation of stamens and styles, and all three of the tritonias (*Tritonia crocata, T. deusta* and *T. squalida*) are pollinated solely by hopliines (Goldblatt *et al.*, 1998). In *Sparaxis grandiflora* flowers often offer nectar and may be strongly scented (subsp. *violacea*), and only subsp. *grandiflora*, which has plum-purple tepals with a white centre is, as far as known, exclusively pollinated by hopliines. Subspp. *fimbriata* and *acutiloba*, which have white or yellow tepals usually with dark marks at the tepals bases and also offer nectar are visited by a range of insects, including hopliines, large-bodied bees, and horseflies.

Four other species of *Sparaxis* have flowers that appear ideally adapted for hopliine pollination. S. *elegans*, *S. pillansii* and *S. tricolor* (Fig. 4) have radially symmetric flowers, and stereotypical beetle marks, and although all are pollinated by large, dark coloured hopliines they are also visited by the short-proboscid horsefly, *Philoliche atricornis,* which forages for the traces of nectar present in the short perianth tube (Goldblatt *et al.*, 2000a). As both hopliine and horsefly visitors carry visible loads of *Sparaxis* pollen (a striking dark purple in *S. elegans*), and contact the stigma lobes, we infer that these species have a bimodal pollination system (sensu Manning & Goldblatt, 2005), one adapted for two different pollinator groups. *S. pillansii* is visited not only by hopliines and horseflies but often by small empidid flies (Empididae) (Goldblatt & Manning unpubl.), which carry visible loads of its pollen and are very likely effective pollinators of the species, but in light of the prominent beetle marks in that species, it is not clear whether these flies, which in some years are abundant, are legitimate pollinators. Not yet investigated for its floral biology, *S. maculosa* has unscented, yellow flowers with a black centre and is likely to be pollinated by hopliines.

In *Ixia,* flowers of which are ancestrally radially symmetric, hopliine pollination appears to have evolved independently at least four times.

Fig. 5. *Ixia cf. dubia*, one of the many beetle pollinated species of *Ixia,* and a visiting hopliine in typical position with its head directed toward the flower centre. Fig. 6. Deep, iridescent red flowers of *Babiana villosa* with enlarged, almost black, anthers providing beetle marks.

In sect. *Ixia* (Fig. 5) all but one of the estimated 22 species are inferred to be adapted for hopliine pollination and have typical features of the pollination system: upright flowers, spreading tepals with contrasting darker or lighter central markings, and absence of nectar (Goldblatt & Manning, 2011). The perianth tube, usually hollow and containing nectar in the genus, is blocked in members of the section by thickened walls tightly clasping the style, and serves only as a flower stalk. Hopliine pollination has been confirmed for 11 species (Goldblatt *et al.*, 1998; Manning & Goldblatt, 2007). One more species of the section, *I. superba*, which has scented flowers, unusual for hopliine pollinated species, is visited by hopliines as well as female bees and honey bee workers, which forage for pollen (Goldblatt & Manning, 2004). One species each in two other sections of *Ixia*, *I. amethystina* (sect. *Dichone*) and *I. pavonia* (sect. *Morphixia*) are also pollinated by hopliine beetles (Goldblatt & Manning, 2011). In the remaining sect. *Hyalis*, two species, *I. aurea* and *I. tenuifolia* have flowers with bimodal pollination systems, using hopliines and horseflies, *Philoliche atricornis* in the former and *Mesomyia edentula* in the latter. Both have a hollow perianth tube and offer small amounts of nectar for the horseflies.

Romulea, another genus of Iridaceae in which hopliine pollination is particularly common, has radially symmetric flowers borne close to the ground, rather like *Crocus*. Of the 30 species studied for pollination (out of 83 known for southern Africa) 15 have been found to be visited by hopliines, 11 in combination with bees, mostly worker honey bees and large-bodied anthophorines. Both hopliines and bees carry host pollen and are effective agents of pollen transfer. Four species appear to be exclusively pollinated by hopliines, most prominent among them the western Karoo species *R. komsbergensis, R. monadelpha* and *R. sabulosa* (Goldblatt *et al.*, 2002). Red flower colour is particularly prominent in *Romulea* species visited by hopliines, the flowers sometimes so similar in colour and shape that the species can only be identified by their vegetative features. Particularly striking examples of convergence for floral pigmentation are found in *R. eximia, R. hirsuta* and *R. obscura* (Manning & Goldblatt, 1996).

Most species of the large southern African genus *Babiana* have bilaterally symmetric flowers (Goldblatt & Manning, 2007a) but radially symmetry has evolved multiple times in the genus. *B. villosa* (series *Strictae*) has brilliant red or pink, radially symmetric and nectarless flowers with striking enlarged, dark blue-purple anthers (Fig. 6) providing contrasting colour, and is pollinated solely by hopliines (Goldblatt & Manning, 2007b). Closely related *B. melanops* has similar radially symmetric flowers, pale or dark blue to mauve, always darker in the centre, and enlarged dark anthers. One population has lemon-scented flowers, produces ample nectar in the perianth tube and is visited both by hopliines and large-bodied bees. A second population has odorless flowers with minute traces of nectar and the only insect visitors noted were large, black *Anisonyx ursus* beetles. The interpopulational variation in this species illustrates the lability of pollination systems and the existence of strong local selection by pollinators.

Babiana papyracea (series *Scariosae*), *B. pygmaea* (series *Brevitubae*) and *B. regia* (series *Babiana*) have radially symmetric flowers, the latter two with a dark brown or red centre, and are each believed to be most closely related to species with bilaterally symmetric flowers that are pollinated by large bodied bees (Goldblatt & Manning, 2007b), thus representing independent origins of hopliine pollination. Hopliines also pollinate similar bilaterally symmetric flowers with a more or less radially symmetric perianth (but with unilateral stamens and style) in *B. angustifolia, B. fragrans, B. rubrocyanea*, and *B. stricta*, either in combination with the nectarivorous horsefly *Philoliche atricornis* or various bees, including *Apis mellifera* and *Anthophora* species, a pattern not uncommon in the southern African flora (Goldblatt *et al.*, 1998; 2000a). These species have bimodal or generalist pollination systems. Exclusive hopliine pollination evidently evolved at least four times in *Babiana* (Goldblatt & Manning, 2006) and mixed hopliine and bee or horsefly systems may have evolved independently in at least two more.

In light of the frequency of hopliine pollination in other large genera of Iridaceae, it is striking that *Gladiolus*, the largest by far with over 160 species in southern Africa, has no species adapted exclusively to hopliines although it exhibits a wide range of other specialized pollination strategies (Goldblatt *et al.*, 2001). The majority of *Gladiolus* species are pollinated by nectar-feeding apid and anthophorine bees but some red-flowered species are pollinated by the large butterfly, *Aeropetes* (Johnson & Bond, 1992), and others by long-proboscid flies, moths, or birds. Hopliines have been captured only on *G. meliusculus*, which has strongly sweet scented flowers and offers ample nectar. The flowers are unusual only in having particularly prominent dark nectar guides that mimic the pattern on co-blooming *Romulea* species that are pollinated exclusively by hopliine beetles. We infer that *G. meliusculus* has a bimodal pollination system using both hopliines and large-bodied bees for pollen transfer.

Hesperantha, with some 82 species (Goldblatt & Manning, 2007c), has unusually few species visited by hopliines despite its radially symmetric flowers. Only *H. vaginata* is known to be exclusively pollinated by hopliine beetles and the bright yellow flowers almost always have conspicuous dark brown markings on the tepals (Goldblatt *et al.*, 2004; Van Kleunen *et al.*, 2007). Closely allied *H. karooica* may also be pollinated by hopliines but its similar flowers lack contrasting markings. Surprisingly, two species of hopliine beetles have been captured on *H. baurii*, an eastern southern African species, which has moderate sized pink flowers. This may be the only record of hopliine visitors outside the southern African winter-rainfall zone.

Several species of bees also visit and pollinate flowers of *H. baurii*, which have no apparent adaptations to attract hopliines. Nevertheless, their horizontally spreading tepals serve as an ideal platform for hopliine assembly. Visits by hopliines to the small flowers of other *Hesperantha* species (Goldblatt *et al.*, 1998) are likewise probably not significant.

In *Geissorhiza*, with over 90 species, hopliine pollination is also evidently rare but three species of hopliines, *Anisochelus inornatus, Anisonyx hilaris* and *A. ignitus* have been captured on flowers of *G. cantharophila*, which is unusual in the genus in having upright flowers with a dark centre and short styles. For the same reason hopliine pollination is inferred for *G. tricolor* (Goldblatt & Manning, 2009). In addition, *Anisonyx ursus* has been recorded on flowers of *G. aspera* and *G. monanthos* (Marloth, 1915; Goldblatt *et al.*, 1998) and other hopliines on those of *G. heterostyla* but the significance of these visits is uncertain: more often all three species receive visits from bees. The small flower size and half nodding orientation of these and several other species of *Geissorhiza* with radially symmetric flowers appear poorly suited to hopliine visits.

In *Lapeirousia* we suspect that *L. azurea* is adapted, at least in part, for hopliine beetle pollination. The large, deep blue flowers have widely cupped, subequal tepals with dark red to almost black markings confined to the lower tepals. The hopliine, *Lepithrix cf. lineata*, has been captured at one site visiting its flowers (new observations) but large anthophorine bees also visit and pollinate *L. azurea* (Goldblatt *et al.*, 1995), which does offer nectar and may have a truly bimodal pollination system. Lastly for Crocoideae, hopliine pollination has been recorded in two species of the small genus *Thereianthus* (11 spp), *T. ixioides* and *T. racemosus*. Two hopliine species have been were captured on *T. ixioides,* and individuals of one of them moved indiscriminately between the flowers of this and the remarkably similar blooms of *Ixia metelerkampiae*, the pale mauve flowers of which also have a dark centre (Goldblatt *et al.*, 2000b), a likely example of Batesian mimicry. Flowers of *T. ixioides* offer small amounts of nectar, visible at the mouth of the perianth tube, suggesting that the species offers a secondary reward and may have a more generalist pollination system than nectarless *I. metelerkampiae*. *Thereianthus racemosus* also receives visits from the hopliine beetle, *Khoina bilateralis* (Goldblatt *et al.*, 1998) but this species also produces traces of nectar and has a strong floral scent and thus likely to have alternative pollinators, probably various bees.

Hopliine pollination also occurs in two other subfamilies of Iridaceae in southern Africa. In *Moraea* (Iridoideae), the so-called peacock moraeas, *M. villosa* and its allies (sect. *Vieusseuxia*), have particularly broad, spreading outer tepals providing a platform for hopliine assembly, and very prominent, darkly pigmented and hairy markings close to the tepal bases, the beetle marks (Fig. 7). Recorded hopliine visitors on *M. tulbaghensis* include *Lepithrix ornatella, Monochelis steineri,* and *Peritrichia abdominalis* at two sites (Steiner, 1998a) and *Anisochelus inornatus*, *Argoplia glaberrimus, Heterochelus detritus,* and *Monochelus steineri* at another site, as well as occasional visits by *Apis* workers (Goldblatt *et al.*, 2005), the latter evidently casual visitors. Hopliine pollinators of *M. villosa,* all from near the town of Malmesbury, include *Anisochelus inornatus, Anisonyx ditus, A. ursus*, *Lepithrix lebisii, L. ornatella*, and *Peritrichia rufotibialis* and from near Tulbagh by one more, so far unnamed *Anisonyx* species. Examples from these last two *Moraea* species demonstrate that multiple species of hopliines visit a particular plant species and that different hopliines visit the same plant species at different sites. Several more species of sect. *Vieusseuxia* are exclusively pollinated by hopliines, including *M. bellendeniii*, *M. cantharophila* and *M. insolens*.

In *Moraea* sect. *Homeria*, two species with painted bowl-type flowers (sensu Bernhardt, 2000), *M. elegans* and *M. comptonii*, are visited by hopliines but the flowers of both species are also strongly scented and offer nectar, and it is no surprise that they are also visited by large-bodied bees, including worker honey bees, and sometimes species of muscid flies, thus providing another example of a generalist pollination system emphasizing hopliines. Other species of sect. *Homeria* have smaller flowers without obvious beetle marks, and both hopliines and other insects, usually bees, have been implicated in the pollination of *M. collina, M. ochroleuca* and *M. vallisbelli.*

The purple or red flowered species of the *Moraea* sect. *Galaxia*, which also have painted bowl-type flowers and lack nectar are likely candidates for hopliine pollination but this has only been confirmed for *M. versicolor* (Manning & Goldblatt, 2007).

Fig. 7. The orange-flowered morph of *Moraea villosa* with iridescent green beetle marks on the outer tepals and a visiting hopliine covered in *Moraea* pollen, brushing against an anther as it clambers across the flower. Fig. 8. *Baeometra uniflora* with orange flowers marked with dark brown beetle marks at the tepal bases and brown *Peritrichia abdominalis* clambering over the centre of the flowers.

Lastly for Iridaceae, *Aristea* (Aristeoideae) also provides some striking examples of hopliine pollination. Most species of this widespread sub-Saharan African and Madagascan genus have short-lived, small, radially symmetric flowers without visible markings, lack nectar or scent, and are pollinated by pollen-collecting female bees (Goldblatt & Le Thomas, 1997; Goldblatt & Manning, 1997a). Several species of subgen. *Pseudaristea*, however, have larger, longer-lived flowers, paler in colour and with dark markings of various kinds. One of the most unusual is *A. lugens*, which has markedly smaller, darkly pigmented outer tepals, often almost black, which provide the contrasting beetle marks for the larger, white or pale blue inner tepals (Fig. 1). Hopliine pollination has been confirmed for this and three more species of the subgenus (Goldblatt *et al.*, 1998). Two of these, *A. teretifolia* and *A. cantharophila*, have dark markings on some or all of the tepals but in *A. biflora* the outer tepals have transparent windows near the base. Viewed from above, the windows constitute dark markings contrasting with the otherwise pale blue perianth (Goldblatt & Manning, 1996; 1997b; Goldblatt *et al.*, 1998). *A. biflora* is also visited by pollen collecting, worker honey bees, evidently attracted by the copious yellow pollen. Lastly, *A. nigrescens* provides a novel adaptation for pollinator attraction. The reverse of the outer tepals are almost black in colour and when in bud represent beetle marks for the open flowers which appear uniformly white or pale blue seen from above. The species is pollinated by the hopliines *Anisonyx ditus* and *A. ursus* (Manning & Goldblatt, 2007).

Of the nine known species of subgen. *Pseudaristea*, four are confirmed as pollinated exclusively by hopliine beetles and one is pollinated by hopliine and worker honey bees. Of the remaining species, two have typical, small blue *Aristea*-type flowers and the third, *A. spiralis* has large, nodding, blue or white flowers without dark markings, offers nectar and is pollinated by long-proboscid horseflies (Johnson, 1992). The variation in structure of the beetle marks in *Pseudaristea* makes it likely that hopliine pollination evolved more than once in the subgenus.

Several other families of geophytic monocots have species adapted for hopliine pollination. In Colchicaceae, *Baeometra uniflora* (Fig. 8) has orange flowers with a dark brown centre and is the only southern African member of the family pollinated exclusively by hopliine beetles (Manning & Goldblatt, 2011). Hopliines have also been noted on another species of the family, *Wurmbea punctata*, which has small, white or pink tepals without beetle marks, and may constitute part of a range of insects that pollinate the species.

Hopliine pollination is restricted in Hypoxidaceae to just three species of *Spiloxene*, *S. canaliculata* and forms of *S. capensis* and *S. serrata* with flowers with dark markings at the bases of otherwise white (rarely pink), yellow or orange tepals. Particularly striking are the iridescent green marks on the tepals in some populations of *S. capensis* (Fig. 9) which are pollinated by the iridescent green *Anisonyx longipes*, while other populations with brown or black tepal markings and are pollinated by similarly dull-coloured hopliines, including *Lepithrix* sp. Some populations of *S. capensis* have flowers evidently without visible markings but they too are frequently visited by hopliines, which have also been captured on the mostly uniformly yellow flowers of *S. serrata*

Fig. 9. *Spiloxene capensis* with dark purple-black and iridescent green beetle marks and visiting *Anisonyx longipes* almost the same colour as the floral markings. Fig. 10. *Ornithogalum dubium*, the white flowers with darker centre and a visiting hopliine, *Peritrichia* sp.

(Goldblatt *et al.*, 1998). Although hopliines accomplish pollination in this species, we infer that it is visited by a range of other insects.

In Hyacinthaceae, *Ornithogalum dubium* (Fig. 10) has white, yellow or orange flowers, often with a dark centre, and is often seen with resident hopliine beetles which readily accomplish pollen transfer from the flowers of one plant to another (Goldblatt *et al.*, 1998). Hopliines have also been noted on flowers of *O. thyrsiflora*, which has a dark ovary, and may also be adapted for hopliine pollination. A very prominent dark eye is developed in *O. ceresianus*, which is almost certainly visited by hopliines. The only other species in this fairly large southern African family pollinated by hopliines is the acaulescent *Daubenya aurea*. The brilliant scarlet or yellow inflorescence in this species is a remarkable example of a daisy-like pseudanthium, in which the false rays are formed by asymmetrical enlargement of the lower flowers in the capitate raceme. The flower heads are heavily visited by hopliines but the abundant pollen produced by the anthers is also collected by moderate-sized andrenid and halictid bees, suggesting that it too has a bimodal pollination system.

Orchidaceae, species of which have complex, bilaterally symmetric flowers, offer few instances of pollination by beetles but the southern African *Ceratandra grandiflora* has been shown by Steiner (1998b) to be pollinated by two hopliine species. The sulphur-yellow flowers of *C. grandiflora* are aggregated in a large, flat-topped corymb and the oil secreting glands, present in other species, are vestigial. *Disa elegans*, another striking exception in the Orchidaceae in southern Africa, has similar capitate inflorescence of white flowers marked with maroon blotches, and is also pollinated by hopliines as well as a species of ceratonine beetle (Steiner 1998b; S.D. Johnson, pers. comm. 2011).

Except in Asteraceae, exclusive hopliine pollination appears to be rare in the dicots, but hopliines are often seen a visitors to inflorescences of genera of several families including *Agathosma* (Rutaceae), Apiaceae and Bruniaceae, the flowers of which show none of the adaptations associated with hopliine pollination in the monocots, and in which the more or less flat topped or massed inflorescences merely provide an area for their assembly. Moreover, these species are visited by a range of other insects. Specialist hopliine pollination is developed in a few members of the large genus *Wahlenbergia* (Campanulaceae), most species of which are pollinated by bees and masarine wasps (Gess, 1999). A few winter-rainfall species with pale blue flowers and dark blue markings or grey centres are likely candidates for this pollination system but to date only *W. capensis* (Goldblatt *et al.*, 1998) and a second species, so far unnamed (new observations), have been confirmed as pollinated by hopliines. One species of the related genus *Prismatocarpus*, the shrubby *P. pedunculatus*, has also been recorded as pollinated by hopliine beetles. As in *W. capensis*, the pale blue corolla has conspicuous, dark blue markings. Lastly for Campanulaceae, several species of *Roella* (Fig. 11) have painted bowl-type flowers strongly suggesting hopliine pollination but their floral biology remains to be investigated. Species Aizoaceae: Mesembryanthemoideae, including species of *Carpobrotus*, also receive visits from hopliines but only casual mention of this is currently available in the literature.

Some larger-flowered *Drosera* species (Droseraceae) are likely to be exclusively pollinated by hopliine beetles, notably *D. cistiflora* (Fig. 2) and *D. pauciflora*, which comprise guilds with co-blooming hopliine pollinated species of *Aristea* and *Moraea* species (Goldblatt & Manning, 1996; Goldblatt *et al.*, 1998).

Fig. 11. *Roella incurva*, a likely hopliine pollinated species, with dark blotches on the petals evidently to attract hopliine visitors. Fig. 12. Striking *Monsonia speciosa*, the only southern African member of Geraniaceae known to be pollinated by hopliines, has pale petals dark at the base and dark stamens and styles that form a beetle mark.

The geophytic *Monsonia speciosa* (Geraniaceae), which has pale to deep pink flowers with darker pigmentation at the base of the petals and on the stamens (Fig. 12), is often seen with resident hopliines and may be exclusively or partially pollinated by these beetles (Goldblatt *et al.*, 1998). No other southern African Geraniaceae are currently known to be pollinated by hopliines.

Lastly, among the dicots, one species of *Nemesia* (Scrophulariaceae), *N. barbata*, an annual, is strongly adapted for hopliine pollination. The enlarged lower lip in this species is dark blue to almost black and densely hairy at the base, providing a striking resemblance to a single large hopliine. Beetles visiting the flowers orient their bodies facing toward the small, pale upper lip and brush against the anthers and or protruding stigmas, and departing beetles invariably bear a zone of pale pollen on the frons that they carry to flowers of neighboring individuals (new observations). A few other species of *Nemesia*, notably *N.strumosa* and its allies (*N. aurens* Grant *ms.*, *N. glandulosa* (E. Phillips) Steiner *ms.* and *N. regalis* Steiner *ms.*) also appear adapted for hopliine pollination, having saccate flowers with a wide, dark throat. Other species of *Nemesia* are evidently pollinated by large-bodied bees. The few *Nemesia* species and the two *Wahlenbergia* species discussed above are the only examples we know of annuals that appear to be specifically adapted for pollination by hopliine beetles. Pollination of annual Asteraceae visited by hopliines is too poorly understood to be included in this category although some annual species of *Ursinia* are likely candidates for hopliine pollination.

Conclusions

Although hopliine beetles are a predictable part of generalist entomophily in the flora of southern Africa they are the primary or sole pollinators of over 75 specialist species in at least 10 plant families, and constitute an active selective force in floral evolution. (Table 1)

Table 1. Families and genera in which hopliine beetles are currently known to constitute part of the legitimate pollinator spectrum.

Family	Genera	Number of species
Aizoaceae	Few documented, including *Carpobrotus*	Unknown
Asteraceae	*Arctotheca, Arctotis, Gazania, Ursinia*, several other genera	? several, not well documented
Campanulaceae	*Prismatocarpus*, ?*Roella*, *Wahlenbergia*	3
Colchicaceae	*Baeometra*, ?*Wurmbea*	2
Droseraceae	*Drosera*	2
Geraniaceae	*Monsonia*	1
Hyacinthaceae	*Daubenya, Ornithogalum*	3
Hypoxidaceae	*Spiloxene*	2
Iridaceae	*Aristea, Babiana, Geissorhiza, Gladiolus, Hesperantha, Ixia, Lapeirousia, Moraea, Romulea, Sparaxis, Thereianthus, Tritonia*	±55
Orchidaceae	*Ceratandra, Disa*	2
Scrophulariaceae	*Nemesia*	±5

Species of Aizoaceae and Asteraceae are typically visited by a range of other insects.

Pollination by hopliines conforms to a pattern quite distinct from classical cantharophily in the magnoliid angiosperms (Faegri & van der Pijl, 1979; Bernhardt, 2000), notably in their preference for brightly coloured flowers lacking floral odour. Hopliine pollination in southern Africa does, however, closely parallel beetle pollination in the eastern Mediterrean, where red flowers with darker centres form a guild pollinated by unrelated *Amphicoma* beetles (Dafni *et al.*, 1990).

Hopliine pollination in the southern African flora is strongly associated with Iridaceae in the winter-rainfall region. It has evolved independently (at least twice) in Hyacinthaceae and many times in Iridaceae, often repeatedly within a single genus. It has contributed significantly to floral diversification in the family, most notably in genera in which it has driven the evolution of radially symmetric flowers from bilaterally symmetric ancestors. This pattern is contrary to widely accepted belief that radially symmetric flowers are invariably plesiomorphic.

The pollination of flowers by hopliine beetles in southern Africa appears to have shaped the flora in two ways. At a superficial level, it helps explain the unusually brilliant and broad range of floral colors and contrasting patterns in the flora in general, but at a more fundamental level, competition for hopliine beetles as pollinators has encouraged both adaptive radiation and convergent floral evolution in several plant families, in particular the Iridaceae.

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716. SPILOXENE CAPENSIS
Hypoxidaceae

Graham Duncan and Allan G. Ellis

Summary. Details of the history, life cycle, distribution, habitat and cultivation requirements of the South African *Spiloxene capensis* (L.) Garside are given, together with a watercolour plate and photographs in habitat.

The plant illustrated here and now known as *Spiloxene capensis* was originally described as *Amaryllis capensis* L. in the 18th century publication *Plantae Rariores Africanae* (Linnaeus, 1760). According to Robert Sweet in his *Hortus Botanicus* published between 1826 and 1827, it was first cultivated in England in 1752. It was later introduced and successfully cultivated at Kew in 1778 from corms sent by Francis Masson from the Cape. In the early 18th century a watercolour painting of the plant was made for the *Flora Capensis* of Jakob and Johann Philipp Breyne that was bound in 1724 and published more than 2 ½ centuries later by The Brenthurst Press (Gunn & du Plessis, 1978). The plant was illustrated on plate 662 of *Curtis's Botanical Magazine* in 1803 from a cultivated specimen, and painted at the Cape in 1834 by Lady Margaret Herschel, wife of the British astronomer Sir John Herschel, published much later, again by The Brenthurst Press (Warner & Rourke, 1996). In 1932 the German botanist Marloth illustrated it in the fourth volume of his *The Flora of South Africa*, and provided an interesting account of its iridescence.

The generic name *Spiloxene* was coined by the English botanist R.A. Salisbury in 1866 and is derived from the Greek *spilos*, a spot, and *xeno*, a host, and refers to the prominent dark spot seen at the tepal bases in most forms of *S. capensis*. Certain members of this genus were previously placed in *Hypoxis* L. and *Ianthe* Salisb., but the South African members were transferred to *Spiloxene* Salisb. by H.G. Fourcade (1932) and S.A. Garside (1936). The genus was last revised by G. Nel (1914) and there are currently thought to be about 30 species, two of which were recently described by D.A. Snijman (2006) from the north-western Cape.

In his account of *Spiloxene* in the *Journal of Botany*, Garside referred to material of *S. capensis* in N. L. Burmann's herbarium at the Botanic Gardens in Geneva, which he believed to have been annotated by

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Plate 716 *Spiloxene capensis* GEORITA HARRIOTT

Linnaeus, and considered to include the type material (Garside, 1936). However, it has been established that none of the seven sheets in Geneva are annotated by Linnaeus and the name remains untypified at present as the original specimen has not been traced (Jarvis, 2007). Four varieties of *S. capensis* were mentioned in a paper by Garside, read at a meeting of the Linnean Society in London in November 1923, but none of these were included in his later treatment of the species occurring on the Cape Peninsula, probably on account of the large number of varying, and not always easily distinguishable colour combinations that had been recorded by that time (Garside, 1950).

Spiloxene has a disjunct distribution in southern Africa and Australia. It is centred in the south-western part of the Western Cape and ranges to the Northern and Eastern Cape in South Africa (Snijman, 2006). *S. scullyi* (Baker) Garside extends to southwestern Namibia (Burke & Mannheimer, 2004), as does *S. alba* (Thunb.) Fourc., and there are several species in Australia, currently still classified under *Hypoxis* (Henderson, 1987). The closely related *Hypoxis*, a large genus of more than 70 species widely distributed in Africa, North and South America, South East Asia and Australia, has about 40 species in southern Africa, and differs from *Spiloxene* mainly in having pubescent leaves and stems, and beaked fruits.

Spiloxene capensis is undoubtedly the most striking species; certain forms of it produce the largest flowers in the genus, and it is extremely variable in tepal length, colour and markings. Tepal length varies from 15 to 50 mm long and tepal colour is rarely plain white or yellow, more frequently white, yellow or pink with a prominent black or dark purple spot at the base of all, or just three of the tepals, or with an iridescent zone below the spot (Fig. 1 & 2). *S. capensis* is the only member of the genus possessing iridescence, seen as a deep blue or emerald green triangular zone. The lower tepal surfaces are light green with reddish or mauve striations. Forms with iridescence are appropriately known as PEACOCK FLOWER or POUBLOM (Afrikaans) in the vernacular.

The new leaves of *Spiloxene capensis* emerge in a basal cluster in late May and early June after autumn and early winter rains. Rapid vegetative growth continues throughout the winter months and flower buds appear at any time from late July to mid-October, and at high

Fig. 1. A white form of *Spiloxene capensis* with blue iridescence in habitat near Darling in the south-western Cape. Photograph: Graham Duncan.

altitude these may emerge as late as December (Garside, 1950). One flower is produced per inflorescence but a number are produced at the same time, or in succession. The flowers only open fully on hot, still days, remaining tightly closed in cold and rainy weather. The erect, cylindrical seed capsules ripen within a few weeks and have circumscissile dehiscence so that the top comes off like a lid, and the seeds are locally dispersed through the shaking action of wind. The corm is replaced annually, but the old corms are persistent underneath the youngest (new) corm, allowing the approximate age of the plant to be determined (Thompson, 1969). The leaves of most forms die off in early summer and the corms undergo a dry dormant period of at least 5 months.

Fig. 2. A yellow form of *Spiloxene capensis* without iridescent spots, in habitat near Fernwood in the south-western Cape. Photograph: Graham Duncan.

This species and the similar *Spiloxene canaliculata* Garside are sometimes confused, but the latter is distinguished by its narrower, recurved leaves that are U-shaped in cross section with no midrib, and in its often longer, usually orange or rarely yellow tepals with dark brown, non-iridescent bases, and in its distinctive J-shaped seeds.

Spiloxene capensis is confined to the Western Cape Province and occurs from the Cape Peninsula north to Clanwilliam in the Olifants River Valley and east to Oudtshoorn in the Little Karoo. Although parts of its habitat have been lost to agriculture, road construction and urban development, the species is not yet considered threatened, by virtue of its wide distribution.

Most spiloxenes are bee-pollinated, but the dark central spots in flowers of the unscented *Spiloxene capensis, S. canaliculata* and *S. serrata* (Thunb.) Garside belong to the guild of plants pollinated mainly by monkey beetles (family Scarabaeidae) (Steiner, 1998). These hairy beetles with strong hind legs feed on the pollen that becomes transferred to the prominent stigmas as they clamber about. We have also observed small, narrow black beetles (possibly soft-winged flower beetles of the family Melyridae, Mike Picker, personal communication) and iridescent chrysomelid beetles feeding on pollen of *S. capensis* near Darling and Stellenbosch in the southwestern Cape.

The accompanying painting by Georita Harriott was painted in 2010 from specimens grown in the University Botanic Garden, Cambridge.

Cultivation. Forms of *Spiloxene capensis* with the iridescent green or blue sheen are the most desirable ones for cultivation and are not more difficult to grow than those without this alluring feature. Although the species occurs naturally in places which are very wet in winter, its corms are extremely sensitive to summer moisture and must be kept as dry as possible during this period. In winter rainfall parts where temperatures do not fall below 5°C for long periods, it can be grown in sunken wire baskets in dedicated pockets in the front rockery but it is more successfully maintained in 20–25 cm diam. plastic containers. It requires an acid medium such as equal parts of coarse river sand and finely sifted compost or milled bark, and the corms are planted 2–3 cm deep in autumn. Plants require full sun or as much bright light as possible, and regular heavy drenching throughout the growing period, especially at flowering (Duncan, 2010). A deep, water-filled saucer helps prevent excessive desiccation of the growing medium during the growing period. Just a single period of excessive desiccation can result in flower bud abortion and plants entering dormancy prematurely. As soon as the leaves start turning yellow in late spring, all moisture should cease and the containers be dried off completely. In suitable conditions, the plants are long-lived in cultivation; a collection I made at Durbanville east of Cape Town in 1984 (*Duncan* 105, in NBG) is still extant in the bulb nursery at Kirstenbosch.

Propagation is achieved by separation of corm offsets in late summer or early autumn, and by seeds sown in autumn. The shiny black seeds are sown 2–3 mm deep in pots or seed trays, placed in bright light and watered regularly with a fine rose cap. Care must be taken not to sow the fine seeds too deeply or too thickly, and seedlings should remain in their containers for at least two seasons before potting-on into individual containers (Du Plessis & Duncan, 1989). Germination of fresh seeds takes place within 3 weeks and seedlings will flower in their third spring season, if well grown.

Spiloxene capensis (L.) Garside, Journal of Botany (London) 74: 267 (1936).

Amaryllis capensis L., Plantae Rariores Africanae: 10 (1760). Type: not designated, original material not traced (Jarvis, 2007). Habitat ad Cap. b. Spei (Species Plantarum ed. 2, 1: 420 (1762)).

Fabricia stellata Thunb., in Fabricius, J.C., Reise Norwegen: 27 (1779). Type: South Africa, Cape, precise locality unknown, Herb. Linn. 427.8.

Spiloxene stellata (Thunb.) Salisb., Genera of Plants: 44 (1866).

Hypoxis stellata (Thunb.) L.f., Supplementum Plantarum: 197 (1781).

DESCRIPTION. *Deciduous, winter-growing geophyte* 100–350 mm high. *Corm* subglobose, 8–20 mm in diam., white, surrounding fibres coarse, reticulate, light to dark brown, produced into a fasciculate neck; old corms disc-like, forming persistent stack beneath youngest corm; roots fibrous with one or more contractile, white. *Cataphyll* lanceolate, upper portion aerial, 10–15 mm long, keeled, lower surface maroon, upper surface white-streaked. *Leaves* 2–8, linear, 90–350 × 3–15 mm, V-shaped in cross section, deeply keeled, midrib prominent on lower surface, spreading to suberect, margins entire or minutely toothed, slightly thickened. *Inflorescence* one-flowered; scape erect, 50–200 mm long, hollow; leaf-like bract produced at node, tightly sheathing, green, margins dark brown; pedicel light to deep brown shading to green above, up to 150 mm long. *Flowers* actinomorphic, stellate, remaining tightly closed in cold or rainy weather; tepals 6, lanceolate, 15–50 × 5–10 mm, upper surface bright white or yellow, occasionally pink, unspotted or with a prominent black or dark purple spot near the base and sometimes a blue or green iridescent zone below, lower surface light green with reddish or mauve striations. *Stamens* 6, erect; filaments 1–2 mm long, black; anthers linear, basifixed, pollen yellow. *Ovary* clavate, trilocular, ovules numerous; style short; stigma lobes 3, broad. *Fruit* a cylindrical capsule 20–28 mm long, dehiscence circumscissile. *Seed* globose, minute, numerous, glossy, black, minutely tuberculate.

DISTRIBUTION. Cape Peninsula to Olifants River Valley and Little Karoo in Western Cape, South Africa.

HABITAT. Seasonally inundated flats, alongside streams and on damp mountain slopes, rarely in pine woods, in clay or sandy soils, in full sun or light shade.

FLOWERING PERIOD. Mainly late July to mid-October, rarely to December, with a peak in September.

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GEISSORHIZA RADIANS
Iridaceae

Graham Duncan

Summary. The striking, threatened South African geophyte *Geissorhiza radians* (Thunb.) Goldblatt is described, together with details of its history, life cycle, distribution, habitat and cultivation requirements.

The splendid contrast in tepal colouration of *Geissorhiza radians* makes it one of the most desirable members of this entirely southern African, winter-growing genus of about 100 species. It was the Swede Carl Peter Thunberg who first collected plants at an unrecorded locality at the Cape, sometime between 1772 and 1775, but at least 20 years elapsed before he formally described it, as *Ixia radians* Thunb. It appeared in an article titled *Novae Species Plantarum Capensium examinatae et descriptae a C.P. Thunberg*, in which 60 new species of Cape plants representing 19 families were published in the German periodical *Phytographische Blätter,* of which only one issue was ever printed, and very few copies are still extant (Thunberg, 1803).

The genus *Geissorhiza* was established by the English botanist John Bellenden Ker Gawler (1764–1842) when he described the yellow-flowered *G. obtusata* Soland. ex Ker Gawl. in *Curtis's Botanical Magazine* in 1803, a plant that later became known as *G. imbricata* (de la Roche) Ker Gawl. subsp. *bicolor* (Thunb.) Goldblatt, following a comprehensive revision of the genus (Goldblatt, 1985). *Geissorhiza* is almost confined to the winter rainfall zone of southern Africa and extends from around Steinkopf in the southern Richtersveld to the Cape Peninsula, east to Grahamstown and inland to Laingsburg in the south-western Great Karoo. The two subgenera of *Geissorhiza* are set apart by the degree to which the persistent tunics of previous seasons overlap each other. In subgenus *Geissorhiza*, to which *G. radians* belongs, the lowermost portion of each tunic protrudes prominently, whereas in subgenus *Weihea*, the tunics completely cover one another (Goldblatt, 1985).

The generic name is derived from the Greek *geisson*, a tile, and *rhizon*, a root, and alludes to the tile-like overlapping corm tunics that are characteristic of many of the species. The specific epithet *radians* presumably refers to the radiant appearance of the open flowers, and

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its bright, wine-red centres have given rise to the vernacular name CUP OF WINE.

Geissorhiza radians has a somewhat complicated taxonomic history and was for many years well known by an earlier name, *G. rochensis* (Ker Gawl.) Ker Gawl., which later proved to be illegitimate, necessitating the new combination *G. radians* (Thunb.) Goldblatt (1983). Very few illustrations of the plant appear in early botanical works, and apart from one by Sydenham Edwards on plate 598 of *Curtis's Botanical Magazine* (Ker Gawler, 1803), the only other I'm aware of is that of the 19th century artist and writer Jane Loudon, in *The Ladies' Flower-Garden of Ornamental Bulbous Plants*, a collection of 58 hand-coloured lithographs published in London, in which it appears on plate 21 in an artistic arrangement with several other geissorhizas (Loudon, 1841).

Geissorhiza radians is endemic to the south-western part of the Western Cape, where it extends from Darling on the west coast to Klapmuts in the Cape Winelands District, just east of Cape Town, (Fig. 1). Within this area, its occurrence is highly fragmented and probably limited to fewer than 15 sites. Most of its former habitat has been lost to ploughing of its fertile habitat for wheat cultivation and it is suffering further decline due to grazing by livestock, alien plant encroachment, and run-off from pesticides and fertilizers; currently it has a conservation status of Endangered (Raimondo & Helme, 2009). The plants occur in colonies on seasonally wet flats and lower slopes, sometimes in standing water and along watercourses, in gravelly, sandy soils, in full sun. In the Tinie Versfeld Wildflower Reserve near Darling it occurs in Swartland Granite Renosterveld vegetation type (Mucina & Rutherford, 2006), in close association with several other moisture-loving Cape geophytes including *Babiana angustifolia* Sweet, *Corycium orobanchoides* (L.f.) Sw., *Romulea tabularis* Eckl. ex Bég. and *Sparaxis bulbifera* (L.) Ker Gawl, (Fig. 2). Tepal colour in *G. radians* varies slightly in shades of light to deep violet-blue above, with wine-red centres, but isolated albino forms occasionally appear within populations. I have recently crossed two evidently recessive albino individuals, the seedlings of which have all flowered true to type (Fig. 3), (Duncan, 2010).

Geissorhiza radians closely resembles two other striking members of this genus, both of which are Critically Endangered, *G. eurystigma*

Fig. 1. *Geissorhiza radians* on a wet slope in Swartland Granite Renosterveld near Darling, south-western Cape. Photograph: Graham Duncan.

L.Bolus and *G. mathewsii* L.Bolus; they have very similar violet-blue tepals with wine-red centres, and also occur in the Darling area. *G. eurystigma* has similar cup-shaped flowers with rounded tepal

Fig. 2. *Geissorhiza radians* flowering with *Babiana angustifolia* (blue) and the orchid *Corycium orobanchoides* (yellow) in the Tinie Versfeld Wild Flower Reserve near Darling, south-western Cape. Photograph: Graham Duncan.

apices, but has a broader, less well defined white ring separating the red centres from the blue upper parts, and lacks the characteristic deep brown pits situated centrally in the red portion of each tepal in *G. radians*. It differs further in its erect, prominent style with feathery branches and its broader, flat ribbed leaves. *G. mathewsii* differs in its smaller, sub-stellate flowers with acute tepal apices, brighter red centres, without brown pits, broader, flat style branches and broader, strongly ribbed, flat leaves. In October 1988 I made a collection of *G. mathewsii* near Doornfontein in the Darling District where I found it growing together with *G. radians* and the violet-flowered *G. monanthos* Eckl. at the base of a moist hillside, the three species occupying different niches; *G. mathewsii* grew in moist, seepage areas whereas *G. radians* was restricted to lower, much wetter parts, and *G. monanthos* was confined to relatively dry ground.

If sufficient rains fall, *Geissorhiza radians* commences leaf growth in late autumn and early winter, followed by rapid leaf elongation and

Fig. 3. A rare albino form of *Geissorhiza radians* in cultivation in the bulb nursery at Kirstenbosch. Photograph: Graham Duncan.

flowering from mid- to late spring, and the leaves desiccate rapidly as temperatures rise and the soil desiccates in early summer. The oblong capsules contain 30 or more small globose, light brown seeds and split into three sections from the apex down, the sections curling outwards to expose the seeds. Most seeds become dislodged close to the mother plants in gusts of wind, while the base of the stem is still attached to the corm, but the stem detaches as soon as the leaves have turned brownish yellow, and the remaining seeds are dispersed as the infructescence is blown about. The wet, occasionally flooded depressions in which this species grows dry up completely and bake rock hard in summer, forcing the corms into dormancy for at least 6 months until the following autumn.

When grown in open bulb beds in the Kirstenbosch nursery, *Geissorhiza radians*, *G. eurystigma* and *G. mathewsii* are actively visited by worker honey bees that appear to feed on their nectar, and inevitably brush against the stigmas, effecting pollination. The flowers of these three species bear striking resemblance to another iridaceous species from the south-western Cape, *Babiana rubrocyanea* (Jacq.) Ker Gawl., that is native to the same area around Darling, and it too is visited by honey bees at Kirstenbosch. Recorded visitors to the flowers of *G. eurystigma* and *B. rubrocyanea* in their natural habitat are the horsefly *Philoliche atricornis,* small halictid bees visit the flowers of *G. eurystigma,* and hopliine beetles visit those of *B. rubrocyanea*; it is thought that the similarly-coloured flowers of these species may form part of a pollination guild (Goldblatt & Manning, 2006; Goldblatt *et al.*, 2009). Both *G. radians* and *B. rubrocyanea* sometimes occur within very close proximity, such as in the Tinie Versfeld Wildflower Reserve near Darling, although *G. radians* always favours wetter terrain.

Photographing displays of *Geissorhiza radians* on a hot still day in its habitat around Darling is not always pleasurable as the experience is inevitably tempered by swarms of tiny midges ('miggies' in Afrikaans) that are strongly attracted to ears, eyes, nostrils and mouths.

Cultivation. *Geissorhiza radians* is one of the most attractive members of this genus and not very difficult to grow in favourable conditions; it is best suited to cultivation in containers or in raised beds, in order that its strict requirements of winter and spring moisture, and summer drought, can be rigorously maintained (Duncan, 2000). In addition to the usual violet-blue forms, the albino form is equally striking and as easily grown. The tiny corms are wholly unsuited to garden cultivation, and even in dedicated rock garden pockets they soon dwindle due to smothering weeds and pest attack. The plants require at least full morning sun or bright light for as much of the day as possible. This species is half hardy, able to stand temperatures down to 0°C for short periods of a day or two, but in cold climates it has to be grown in a cool greenhouse with adequate ventilation (Duncan, 2010). *Geissorhiza radians* performs well in 20–25 cm diam. plastic containers and likes a mixture of equal parts of finely sifted, well decomposed compost and river sand, with the corms planted in a thin layer of pure river sand, with the top of the corm about 10 mm below the surface. After an initial drench applied in autumn, heavy drenching twice per week is required throughout the growing and flowering periods. In order to ensure the medium remains sufficiently moist, pots can be placed in water-filled saucers, as a single instance of excessive desiccation during the growing period results in rapid flower bud abortion and the leaves turning yellow, resulting in premature dormancy and development of the new corm being adversely affected (Duncan, 2010). After flowering and as leaves naturally start desiccating in late spring, watering must cease completely and the medium be kept bone dry for the duration of the summer dormant period. The plants respond very well to light applications of the granular organic fertilizer, Neutrog Bounce Back, once active growth has begun.

Propagation is by seeds sown in autumn, and by removal of cormlets that develop around the base of the mother corm in late summer. Sow the fine seeds 2 mm deep in the same medium recommended for adult corms, and take care not to sow too thickly, in order to avoid attack by damping-off fungi. Watering regularly with a fine rose cap, or alternatively standing pots in water-filled saucers is recommended as the latter practise avoids disturbance to the germinating seeds. Seedlings generally flower in their second season but *Geissorhiza radians* can flower in as little as 8 months, in ideal conditions.

To form seeds, cross-pollination between different clones is required, but like many Cape dwarf irids, the flowers of *Geissorhiza radians* remain closed in cold, rainy or windy weather, only opening fully on hot, still days; every opportunity to undertake hand-pollination should therefore be taken whenever they arise, in order to ensure a successful seed harvest, as individual flowers last just a few days. It is essential to harvest pure seeds and have new stock coming-on, in the event of loss of mature plants (Duncan, 2000).

The leaves are sometimes stripped by snails, the flower buds are often subject to aphid infestations, and the corms are sometimes plagued by mealy bugs; these three pests need to be controlled as soon as possible as they can transmit viral disease. Fungal rotting of the corms occurs in insufficiently dry summer conditions. The corms are evidently very tasty, as they are relished by porcupines, mole rats and Namaqua rock mice in cultivation in South Africa.

Geissorhiza radians (Thunb.) Goldblatt, Nordic Journal of Botany 3: 441 (1983).

Ixia radians Thunb., Phytographische Blätter 1: 3 (1803). Type: South Africa, Cape, precise locality unknown, *Thunberg s.n.* (UPS, Herb. Thunb. 982, lectotype, designated by Goldblatt, 1983).

Ixia rochensis Ker Gawl., Curtis's Botanical Magazine 17, t. 598 (1803), nom. illeg. et superfl., pro *I. secunda* de la Roche (1766) = *Geissorhiza eurystigma* L.Bolus.

Geissorhiza rochensis (Ker Gawl.) Ker Gawl. var. *rochensis*, Annals of Botany (König & Sims) 1: 224 (1804), nom. illeg.

Ixia larochei Roem.& Schult., Systema Vegetabilium 1: 379 (1817), nom. superfl., pro *I. secunda* de la Roche = *Geissorhiza eurystigma* L.Bolus. *Geissorhiza larochei* (Roem.& Schult.) Loudon, Hortus Brittanicus (edn 1): 16 (1830), nom. illeg.

Geissorhiza rocheana Sweet, Sweet's Hortus Brittanicus (edn 1): 399 (1827). Type: South Africa, Cape, precise locality unknown, figure in Curtis's Botanical Magazine 71: t. 598 (1802).

Geissorhiza cyanea Ecklon, Topographisches Verzeichniss der Pflanzensammlung von C.F. Ecklon: 20 (1827), nom. nud.

Geissorhiza tulipifera Klatt, Abhandlungen der Naturforschenden Gesellschaft zu Halle 15: 390 (1882). Type: South Africa, Cape, near Paarl, *Drège 8486* (B, holotype).

Geissorhiza rochensis (Ker Gawl.) Ker Gawl. var. *spithamaea* (Ker Gawl.) Baker, Handbook of the Irideae: 156 (1892) (= *Geissorhiza eurystigma*). Type: South Africa, Cape, precise locality unknown, *Masson s.n.* (BM, lectotype, designated by Goldblatt, 1985).

DESCRIPTION. *Deciduous, winter-growing dwarf geophyte* 80–150 mm high. *Corm* globose, asymmetric, 5–9 mm in diam., cormlet-forming, tunics woody, imbricate, dark brown. *Leaves* 3, linear, bright green, 50–90 × 0.5–1.7 mm, upper and lower surfaces 2-grooved, margins thickened, lower two leaves basal, upper leaf inserted on stem, inflated below, with a strongly ribbed sheath. *Stem* erect to suberect, 60–90 mm long, slender, bright green, simple or rarely 1-branched. *Inflorescence* a 1–6-flowered spike; bracts 2, lanceolate, papery, 8–15 × 3–5 mm. *Flowers* broadly cup-shaped, zygomorphic, secund, remaining tightly closed in cold, rainy or windy weather; perianth tube broadly cylindrical, 6–8 mm long; tepals obovate, 15–22 × 11–14 mm, upper portion dark violet-blue or pure white, lower half wine-red, streaked reddish brown, with a narrow white or purple upper margin and a large, central, blackish brown pit. *Stamens* declinate, included, filaments equal, 9–11 mm long, curving upwards above, reddish- brown or red; anthers linear, 3 mm long; pollen light brown to orange. *Ovary* oblong, 2–3 mm long, light green; style filiform, 3–4 mm long, arching below stamens, branches 3, recurved, 4–5 mm long, reddish-brown or red. *Fruit* an oblong, membranous capsule 6–7 × 3–4 mm. *Seeds* globose, 0.7 × 0.7 mm, light brown.

Distribution. Darling to Klapmuts in south-western Cape, South Africa.

Habitat. Seasonally inundated flats and along watercourses in gravelly sand, in full sun.

Flowering period. September to October, with a peak in mid-September.

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717. GEISSORHIZA MONANTHOS
Iridaceae

Graham Duncan

Summary. Details of the history, life cycle, taxonomy, cultivation and propagation requirements of the striking *Geissorhiza monanthos* Eckl. from South Africa's southwestern Cape are given, accompanied by a watercolour painting and habitat photographs.

It is surprising that a species of such beauty, ease of cultivation and prolific flowering is so seldom grown today, yet this appears to have been the case historically as well, for no paintings of it are to be found in the 19th century or earlier. The only published watercolour paintings appear to be the recent ones of Elise Bodley on plate 29 of *Bulbous Plants of Southern Africa* (Du Plessis & Duncan, 1989) and Barbara Jeppe on plate 22 of *Spring and Winter Flowering Bulbs of the Cape* (Jeppe & Duncan, 1989).

The species was first described as *Ixia monanthos* by Thunberg in his *Flora Capensis* published in Uppsala in 1811, from material collected at an unrecorded locality at the Cape. However, Thunberg's name proved to be an illegitimate homonym as it had already been used by Daniel Delaroche in 1766 for a plant later placed in the genus *Sparaxis* by N.E. Brown in 1924, and it was C.F. Ecklon who made the new combination in *Geissorhiza*, in 1827 (Goldblatt, 1985).

Like *Geissorhiza radians, G. monanthos* falls within subgenus *Geissorhiza*, but in a different section, *Planifolia,* that is characterized mainly in having flat, smooth leaf surfaces. It is most closely allied to *G. aspera* Goldblatt, a very common species widely distributed in the western part of the Western Cape, which has similar flat leaves and a pubescent stem, but differs in its much smaller, many-flowered spikes of light to deep blue or purple actinomorphic flowers with erect anthers. *G. monanthos* should not be confused with the later-published *G. monantha* Sweet which is a synonym of another blue-flowered species, *G. eurystigma* L.Bolus (Goldblatt, 1985).

Thunberg's specific epithet *monanthos* is descriptive of the solitary-flowered spike produced in some specimens.

Geissorhiza monanthos has dark violet, zygomorphic flowers with a light yellow or cream-coloured translucent throat and a broad

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Plate 717 *Geissorhiza monanthos* GEORITA HARRIOTT

Fig. 1. *Geissorhiza monanthos* with *Romulea eximia* on a wet slope near Darling. Photograph: Graham Duncan.

Fig. 2. *Geisssorhiza monanthos* in Swartland granite renosterveld near Darling. Photograph: Graham Duncan.

iridescent wine-red, dark brown or purple inner ring. The tepals have obtuse apices and the upper tepal is conspicuous in being set apart from the others. The three stamens are distinctively bent downwards, with the middle filament always shorter, and the prominent linear anthers produce reddish brown or sometimes yellowish white pollen. Like those of all geissorhizas, the flowers of *G. monanthos* remain closed in cold, rainy or windy weather, only opening fully on hot, still days.

Recorded pollinators for this species are an unidentified solitary bee (*Andrena* sp.) (family Andrenidae) and the monkey beetle *Anisonyx ursus* (family Scarabaeidae) (Goldblatt *et al.*, 2009a).

The species is native to a small area of the southwestern Cape from Darling on the west coast, inland to Malmesbury and south to Stellenbosch in the Cape Winelands. In the Darling district I have seen *G. monanthos* growing in close association with the Vulnerable *Ixia curta* Andrews, the moisture-loving and endangered *Geissorhiza radians* (Thunb.) Goldblatt and the Critically Endangered *G. mathewsii* L.Bolus, but it always favours less moist terrain than the latter two species.

Geissorhiza monanthos occurs in colonies on flats and lower granite hill slopes amongst low scrub in gravelly sand, (Figs 1 & 2). Near Doornfontein in the Darling district it occurs in the Swartland Granite Renosterveld vegetation type, a critically endangered vegetation unit, 80% of which has been transformed through agricultural expansion and housing development (Mucina & Rutherford, 2006). As a result, populations of *G. monanthos* are coming under increased pressure, and the species currently has a conservation status of Near Threatened (Goldblatt *et al.*, 2009b).

CULTIVATION. Certain large-flowered forms of *Geissorhiza monanthos* from the Darling area are the best ones for cultivation and this species is a very rewarding subject for pots, window boxes and raised bulb frames, but is too fragile to survive the rigours of cultivation in garden beds. The corms are long-lived (up to 10 years) in ideal conditions of cultivation, and at Kirstenbosch I grow it in 20–25 cm diam. plastic pots on raised benches in bright light. The plants perform well in a medium of equal parts finely sifted, well decomposed compost and river- or industrial (silica) sand. The tiny corms are planted 5–10 mm deep and spaced 10 mm apart for massed effect. The plants require a well-ventilated position receiving full morning sun or bright light for as much of the day as possible. Following an initial drench in mid-to late autumn, regular watering twice per week is recommended once the new leaves appear. Like *G. radians*, the plants respond very well to light applications of the granular organic fertilizer, Neutrog Bounce Back, once active growth has begun.

Whereas this species does not require the constant wet conditions needed by *G. radians*, it is important to maintain regular watering throughout the growing period and especially in the period just prior to flowering, to prevent flower bud abortion and the plants entering dormancy prematurely (Duncan, 2010).

In cold climates this species is best suited to the cool greenhouse and it is half-hardy, able to stand temperatures down to 0°C for short periods of a day or two. The flowers require cross-pollination to form seeds and this is easily achieved using a fine water paint-brush. The pollen is ready for use in hand-pollination once it is dry, has turned reddish brown or yellowish white, and easily clings to the paint-brush bristles. It is essential to isolate specimens from other *Geissorhiza* species before the flowers open to prevent the occurrence of hybrids. Once the leaves start turning yellow all watering should cease and the corms kept completely dry until the following autumn. Corms of this species are longer-lasting in cultivation than those of *G. radians*, lasting up to 10 years in ideal conditions.

Geissorhiza monanthos is subject to the same pests that affect *G. radians*, i.e. snails that strip the leaves, aphids that attack developing flower buds and mealy bugs that infest the corms, but is less susceptible to fungal rotting of the corms. In cultivation at Kirstenbosch, the corms are readily taken by porcupines, mole rats and Namaqua rock mice (Duncan, 2010).

Propagation is easily achieved by seed sown in late autumn, and stocks can also be increased by separation of the many cormlets that form in a ring around the base of the mother corm. If sown thinly enough, seeds can be sown directly into permanent containers, obviating the need to lift, separate and replant seedling corms. Sow the seeds 3 mm deep in the same medium recommended for adult corms, and water regularly with a fine rose cap, or alternatively stand the pots in water-filled saucers to avoid disturbing the germinating seeds. Seedlings will certainly flower in their second season but can flower in as little as 7 months, in ideal conditions.

It is important to harvest seeds as soon as the ripe capsules begin to split, as they are readily dislodged in gusts of wind and frequently colonise adjacent pots (Duncan, 2000).

Geissorhiza monanthos Eckl., Topographisches Verzeichniss der Pflanzensammlung von C.F. Ecklon 21 (1827).

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Geissorhiza bellendenii MacOwan, Journal of the Linnean Society (Botany) 25:393 (1890). Type: South Africa, Cape, Groene Kloof near Mamre, *P. MacOwan s.n.* in Herbarium Normale Austro-Africanum (SAM, lectotype).

DESCRIPTION. *Deciduous, winter-growing dwarf geophyte* 60–260 mm high. *Corm* ovoid, 4–6 mm in diam., tunics woody, imbricate, brownish-black, strongly cormlet-forming. *Leaves* usually 3, rarely , linear to narrowly lanceolate, 30–100 × 2–4 mm, erect, surfaces flat with prominent midrib, light green, lower leaf basal, upper leaves inserted on stem, smooth; margins slightly thickened, smooth. *Stem* erect, 50–180 mm long, slender, purplish magenta at base, shading to light green above, minutely pubescent, simple or 1–2-branched. *Inflorescence* a 1–4-flowered, flexuose spike, occasionally 1–2-branched; bracts 2, lanceolate, 8–12 × 2–4 mm, green at base, light brown and papery above. *Flowers* secund, zygomorphic, weakly cup-shaped, remaining tightly closed in cold, windy or rainy weather; perianth tube cylindrical, 1–2 mm long; tepals obovate, 12–18 × 7–12 mm, deep violet, base cream to light yellow, translucent, with an iridescent reddish, dark brown or purple inner ring, apices obtuse. *Stamens* declinate, unilateral, subequal, included; filaments bicoloured, white below, shading to purple above, lateral filaments 6–8 mm long, middle filament 4.5–6.5 mm long; anthers linear, 4–6 mm long; pollen reddish brown, rarely yellowish white. *Ovary* oblong, 2–3 mm long, light green; style declinate, 9–11 mm long, deep purple, branches 3–4 mm long, strongly recurved. *Capsule* oblong, 6–8 × 3–4 mm, membranous. *Seeds* globose, 0.6 × 0.6 mm, light brown.

DISTRIBUTION. Darling to Malmesbury and Stellenbosch in the south-western part of the Western Cape, South Africa.

HABITAT. Low hills and flats in gravelly sand, in full sun.

FLOWERING TIME. Late August to early October, with a peak in late September.

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718. MORAEA ARISTATA
Iridaceae

Graham Duncan

Summary. The striking and highly threatened South African geophyte *Moraea aristata* (D. Delaroche) Asch. & Graebn. is described, together with details of its history, biology and cultivation requirements.

The earliest illustrations of the plant now known as *Moraea aristata* are two watercolour drawings executed for the Florilegium *The Flora Capensis of Jakob and Johann Philipp Breyne* in about 1700. Jakob Breyne (1637–1697), a German merchant and botanist, and his son Johann Philipp (1680–1764), a physician, both established botanical gardens in Danzig through trade with the Dutch East Indies, Japan and southern Africa. The Florilegium, comprising 86 drawings by several artists, was bound in 1724 and finally published more than two and a half centuries later by The Brenthurst Press in Johannesburg (Gunn & Du Plessis, 1978). The stylised, unsigned plates were probably undertaken from wild-collected specimens at the Cape and depict two forms of *M. aristata*, one with typical clear white outer tepals, the other the less common type with blue mottling. The plant was evidently in cultivation in Holland by the 1750s and the first published plates were those of Sydenham Edwards in *Curtis's Botanical Magazine*, illustrated as *Iris pavonia* Curtis in 1791, and one by the Belgian painter and botanist, Pierre-Joseph Redouté, reproduced as *Vieusseuxia glaucopis* DC in the first volume of his *Les Liliacées*, in 1803. A later plate in pencil and watercolour, by the British astronomer Sir John Herschel and his wife Lady Margaret was done from specimens gathered in the grounds of the Royal Observatory (now the South African Astronomical Observatory) in Cape Town in September 1835 (Warner & Rourke, 1996).

In 1758 the Scottish horticulturist and botanist Philip Miller established the genus *Morea* in honour of Robert More of Shropshire, but Linnaeus later altered its spelling to *Moraea,* in order to associate the name with his father-in-law, J. Moraeus, a Swedish physician (Duncan, 2010b). *M. aristata* is a member of subgenus *Vieusseuxia* that includes species with relatively long-lived flowers (lasting 3 days)

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that have much reduced inner tepals, and single leaves. Within this subgenus, *M. aristata* belongs to section *Vieusseuxia* that includes those traditionally known as 'peacock' moraeas which have showy orbicular outer tepals with prominent iridescent spots or 'eyes', outlined in one or more zones of contrasting colour (Goldblatt, 1986). This group includes well known species such as *M. gigandra* L.Bolus, *M. tulbaghensis* L.Bolus and *M. villosa* (Ker Gawl.) Ker Gawl. *M. aristata* most closely resembles *M. villosa* but is distinguished from it mainly in its white tepals, and smooth stem and leaf. Its mode of vegetative reproduction differs from *M. villosa* in its production of cormlets at the tips of subterranean stolons, and it is geographically isolated from *M. villosa* which is absent on the Cape Peninsula.

The genus *Moraea*, with more than 200 species, is widely distributed in sub-Saharan Africa, with outliers in the Mediterranean and the Middle East, but its area of highest diversity is in the winter rainfall zone of the Western Cape, especially in the south-western part of this province. The smaller groups of summer-growing and evergreen groups are native mainly to the Eastern Cape, KwaZulu-Natal, Lesotho and Mpumalanga, and the blue-flowered *M. stricta* Baker has the widest range of all the species, extending from the Eastern Cape to northern Ethiopia (Goldblatt, 1986).

Moraea aristata, the subject of this plate, was first described in 1766 as *Vieusseuxia aristata* by the Swiss botanist Daniel de la Roche from material cultivated in Europe, but was perhaps most well known by one of its later names, *Vieusseuxia glaucopis* DC and by Redouté's famed plate, and it was known under several other names by subsequent authors. The Latinised specific epithet *aristata* is descriptive of the long central lobe of the inner tepals that ends abruptly in a straight point or arista.

This species is endemic to the north-eastern Cape Peninsula, occurring in remnant Peninsula Shale Renosterveld vegetation (Mucina & Rutherford, 2006). It is currently limited to a single subpopulation along the Liesbeek River in the suburb of Observatory, surrounded by urban sprawl. Despite its location within the protected grounds of the South African Astronomical Observatory, it is on the verge of extinction there as the limited number of individuals with their low genetic diversity, poor seed production, and the disturbed site with smothering grass renders this subpopulation non-viable

Plate 718 *Moraea aristata* GEORITA HARRIOTT

(Duncan, 2003). It has a conservation status of Critically Endangered, mainly as a result of urbanisation (Victor *et al.*, 2009). The species has historically always been restricted to clay slopes and flats east of Table Mountain and plants at the Observatory have traditionally been taken care of by a succession of Directors' wives, the current one being Mrs Anne Charles. It is indeed a paradox in view of its dire circumstances in the wild, that *M. aristata* is one of the most obliging members of this genus to grow and has escaped from cultivation and become naturalised in South Australia (Groves *et al.*, 2003), where it may be potentially invasive. Today it survives in cultivation in botanical gardens and private bulb collections in a number of countries.

During the early 1980s I made an attempt with several Kirstenbosch horticultural colleagues to bolster the only remaining subpopulation at the Observatory by planting 200 additional corms that had been propagated in the Kirstenbosch Bulb Nursery, close to the subpopulation. Initially these additional plants performed well, but because all material of this species in cultivation originates from this subpopulation with its limited genetic base, and perhaps because the beetle pollinators no longer exist in sufficient numbers at this site, the number of individuals there has not increased.

Moraea aristata commences vegetative growth in mid- to late autumn once sufficient autumn rains have fallen. Rapid leaf growth ensues throughout winter and the flower buds appear in mid- August, flowering reaching a peak from late August to early September. Each flower lasts 2–3 days but a succession of flowers is produced per plant over a period of about 3 weeks. In early October the ripe capsules split longitudinally for about half their length and the angular, light brown seeds are dispersed locally by the shaking action of wind.

A study of pollination mechanisms in peacock moraeas showed that the orange- or red-flowered *Moraea tulbaghensis* and the purple-, mauve-, pink- or rarely orange-flowered *M. villosa* are visited and pollinated exclusively by hopliine (monkey) beetles of the family Scarabaeidae (Steiner, 1998). I have often observed the monkey beetle *Pachycnema crassipes* Fabricius feeding on pollen of *M. aristata* plants grown in open beds in the bulb nursery at Kirstenbosch. The beetles are attracted to the dark blue iridescent spot located near the base of each of the three broad outer tepals, and certainly in these cultivated plants pollination is effected as pollen deposited onto their heads and backs brushes against the stigma lobes when the beetles enter the flowers of different clones (Duncan, 2010b). At the Observatory site, two as yet unidentified species of cetonid (flower chafer) beetle (Cetoniinae: Scarabaeidae), one of which was covered in pollen, were photographed visiting the flowers of *M. aristata* by the current Director, Prof. Phil Charles, but whether or not these beetles come into contact with the stigmas is unknown.

Cultivation. *Moraea aristata* responds very well to cultivation and flowers prolifically in ideal conditions. The corms are planted in autumn at a depth of about 3 cm in a sandy or clayey medium into which finely sifted, well-decomposed organic matter has been added. They need full sun or as much bright light as can be provided. The plants have a vigorous root system and, when grown in containers, require deep plastic containers with a diameter of 30 cm, in order for them to flower optimally (Duncan, 1983). In temperate climates they can be grown outdoors in deep bulb beds or in dedicated rock garden pockets that are securely lined with wire mesh to exclude mole rats, and kept dry in summer. In addition, the plants can be successfully naturalised in shallow-rooted buffalo grass *Stenotaphrum secundatum* (Walter) Kuntze, provided that it is not watered in summer, and not subject to mole rats and porcupines, (Fig. 1). Corms can be inserted or seeds scattered over the grass in autumn and covered with a 5 mm layer of equal parts river-sand and finely sifted compost (Duncan, 2010a). *M. aristata* is half-hardy and can withstand temperatures down to O°C or 32°F for short periods, but in cold climates it is best suited to the cool greenhouse. Regular heavy drenching is essential during the winter-growing and spring-flowering periods, but the corms must be kept completely dry throughout the summer dormant phase. The plants flower from mid-August to September in the wild but in cultivation they sometimes begin flowering in late July.

Seeds of *Moraea aristata* remain viable for at least 5 years when stored at low temperature, but when stored at room temperature they should be sown in the immediately ensuing autumn following harvesting, failing which viability decreases markedly. Seeds can be sown in deep pots or trays, or directly into deep outdoor seed beds, in the same medium recommended for mature corms. Seeds should be sown at a depth of 3–4 mm, and if fresh, germinate within about 5 weeks. Seedlings should be allowed to grow undisturbed for two

Fig. 1. *Moraea aristata* naturalised in buffalo grass (*Stenotaphrum secundatum*) at Kirstenbosch Botanical Garden. Photograph: Graham Duncan.

seasons before planting into permanent positions at the beginning of their third season, during which some may flower for the first time, if well grown (Duncan, 2010b).

In order to obtain pure seeds from cultivated plants it is necessary to cross-pollinate different clones by hand, as the species is self-incompatible. An anther is located underneath each style branch, and pollen is ready for collection once it has become crumbly, turned orange and easily adheres to a pollination implement such as a water-paint brush. In addition to seeds, *M. aristata* and a few other members of the 'peacock' moraea group are readily propagated by cormlets that form at the tips of subterranean stolons, and these can be removed and potted-up after a single season's growth (Du Plessis & Duncan, 1989).

Moraea aristata is not especially susceptible to pests and diseases although the leaves, stems, flower buds and developing fruits are sometimes subject to aphids, and the leaf undersides sometimes fall prey to attack by red spider mites as temperatures rise in late spring. In susceptible areas, the corms are taken by mole rats and Namaqua rock mice. Fungal rotting of the corms often occurs when they are not kept sufficiently dry during the summer dormant phase.

Moraea aristata (D. Delaroche) Asch. & Graebn., Synopsis Mitteleuropaischen Flora 3: 518 (1906).

Vieusseuxia aristata D. Delaroche, Descriptiones Plantarum Aliquot Novarum: 33 (1766). Type: South Africa, Cape, precise locality unknown, *van Royen s.n.* (L, Herb. van Royen, lectotype, designated by Goldblatt & Barnard (1970).

Ferraria ocellaris Salisb., Prodromus Stirpium 41 (1796), nom. nov. pro *Iris pavonia* Curtis var. Type: South Africa, Cape, precise locality unknown, figure in Curtis's Botanical Magazine 5: t. 168 (1791).

Vieusseuxia glaucopis DC, in Redouté, Les Liliacées 1: t. 42 (1803). Type: South Africa, Cape, precise locality unknown, figure in Redouté, Les Liliacées 1: t. 42 (1803).

Moraea tricuspis (Thunb.) Ker Gawl. var. *ocellata* D.Don, British Flower Garden (series 2) 3: t. 249 (1834). Type: South Africa, Cape, precise locality unknown, figure in British Flower Garden (series 2) 3: t. 249 (1834).

Moraea glaucopis (DC) Drapiez, Dictionnaire Classique des Sciences Naturelles 7:478 (1841).

DESCRIPTION. *Deciduous, winter-growing geophyte* 250–420 mm high. *Corm* globose, 10–15 mm in diam., white, forming cormlets at apices of subterranean stolons; outer tunics strong, brownish cream, apices fasciculate; cataphylls 2, upper cataphyll prominent, fibrous, light brown. *Leaf* 1, linear, 400–550 × 4–7 mm, greenish grey, basal, glabrous, bifacial, apex terete. *Stem* erect to suberect, glabrous; stem nodes 2, prominent; sheathing stem bracts erect, greenish grey, apices attenuate, light brown; outer and inner spathe bracts overlapping. *Inflorescence* a rhipidium, sometimes 1–2 branched, producing several flowers at staggered intervals; flowers iris-like, 3 outer tepals orbicular, 32–35 × 35 mm, spreading, upper surface white, sometimes lightly to heavily blue-spotted, with prominent iridescent blue or green spot at base, outlined in violet and occasionally yellow above, bases black, hairy; lower surfaces white, streaked deep blue; tepal claws suberect, 12–15 × 2–6 mm, upper surface hairy, yellow above, lower surface greenish; inner tepals 3, tricuspidate, 16–21 mm long, outer lobes 2–3 mm long, central lobe 8–10 mm long, aristate, white, heavily brown-mottled. *Filaments* erect, fused into a white column 2–4 mm long; anthers 3, oblong, 5–6 mm long, appressed to style branches; pollen orange. *Ovary* oblong, 8–10 × 2 mm, light green; style white, branches 3, suberect, 7–8 mm long, crests 6, erect, 6–7 mm long, triangular, margins serrated; stigma lobes white. *Capsule* oblong, 15–20 × 4–5 mm, light brown. *Seeds* angular, testa light brown. *Chromosome number*: 2n = 12 (Goldblatt, 1976).

DISTRIBUTION. Confined to one site along the Liesbeek River in the north-eastern Cape Peninsula, surrounded by urban sprawl.

HABITAT. Seasonally moist clay slopes and flats in remnant Peninsula Shale Renosterveld vegetation.

FLOWERING PERIOD. August to September, with a peak from late August to early September.

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719. MORAEA TULBAGHENSIS
Iridaceae

Graham Duncan

Summary. Details of the history, ecology, cultivation and propagation requirements of the spectacular, endangered Western Cape geophyte *Moraea tulbaghensis* L. Bolus are given, accompanied by a colour plate and habitat photograph.

Moraea tulbaghensis was collected and described by the Cape Town botanist Dr Louisa Bolus in 1932, in the south-western part of the Western Cape, near the small town of Tulbagh which prompted the specific epithet. Situated in a bowl surrounded by the spectacular Obiqua, Winterhoek and Witzenberg Mountains, Tulbagh was founded in about 1700 when the Dutch colonial government granted land rights to Dutch and Huguenot settlers. It is renowned for its deciduous fruit orchards and vineyards, Cape Dutch architecture and the 1969 earthquake. Plants of this *Moraea* had, however, first been collected in the early 19th century by that intrepid botanical duo, the Dane C. F. Ecklon and the German C. L. Zeyher. The more robust forms, later known as *M. neopavonia* R. Foster, were collected earlier still, in the late 18th century by C. P. Thunberg (Goldblatt, 1986).

Moraea tulbaghensis is confined to a small area of the western and south-western part of the Western Cape extending from Piketberg to Wellington, in the lower Berg- and upper Breede River Valleys. The plants are very variable with respect to tepal size and shape, and tepal markings vary considerably, sometimes even within the same population. The typical form, such as the one illustrated here, has relatively small, somewhat cupped flowers with more or less orbicular, light to bright orange or rarely brick-red outer tepals with prominent iridescent peacock-green or blue 'beetle spots' outlined in black, whereas the more robust forms previously classified as *M. neopavonia* have much larger, broadly lanceolate bright orange or rarely yellow or white tepals with prominent iridescent navy-blue or emerald green beetle spots, with a broad black zone below. The tepal claws of most forms of this species are bearded above and lightly to heavily spotted with black.

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The plants occur in Swartland- and Breede Shale Renosterveld vegetation, in acidic, stony clay soils (Mucina & Rutherford, 2006). Growing as solitary individuals within large colonies, they favour open flats and lower hill slopes amongst grasses and low bushy cover, in full sun. Occurring in an area notorious for strong wind, the blooms only open fully on hot, still days. Destruction of its fertile habitat through expansion of agricultural fields for cereal crops and fruit orchards has been the major factor in its decline, and to a lesser extent, housing expansion, evident on flats around Gouda, a village to the west of Tulbagh, where a fairly large population grows on flats amongst annual grasses and a bizarre black-flowered pelargonium, *P. auritum* (L.) Willd. var. *auritum*. The species is currently known from only seven severely fragmented subpopulations and currently has a conservation status of Endangered (Goldblatt *et al.*, 2009). Although a red-flowered population occurs within the boundaries of the Elandsberg Private Nature Reserve near Hermon south of Tulbagh, unfortunately this species occurs mainly on privately owned land that is all too often left unprotected, with occasional populations along vulnerable road verges. Fortunately, a good quantity of seeds of *M. tulbaghensis* is preserved in long-term storage within the Millenium Seed Bank at Wakehurst Place.

The fertile flats and lower hill slopes around Tulbagh are home to a multitude of other Cape irids, many of which are now on the Red List as a direct result of habitat loss from ploughing for agriculture, including the spectacular reddish-purple *Sparaxis grandiflora* (D. Delaroche) Ker Gawl. subsp. *grandiflora,* and a number of highly threatened *Ixia* species including the deep crimson or pure white *Ixia campanulata* Houtt., the white, pink or bluish-green *I. rouxii* G. J. Lewis, the purple *I. vinacea* G. J. Lewis and the turquoise *Ixia viridiflora* Lam. (Duncan, 2007).

Moraea neopavonia was formerly recognised as a distinct species, but is now regarded merely as a large-flowered form of *M. tulbaghensis* (Goldblatt & Manning, 2002). Along with all the other moraeas featured in this part of *Curtis's Botanical Magazine*, it is a member of subgenus *Vieusseuxia* that encompasses the 'peacock' moraeas and is most closely allied to *M. villosa* (Ker Gawl.) Ker Gawl., which has a similar pubescent lower leaf surface and stem, but larger blooms in shades of mauve, purple, pink or rarely cream or orange, usually

Plate 719 *Moraea tulbaghensis* GEORITA HARRIOTT

with much longer style crests up to 8 mm long. Reddish forms of *M. tulbaghensis* could be confused with the orange *M. villosa* (Ker Gawl.) Ker Gawl. subsp. *elandsmontana* Goldblatt, but the latter has the large suborbicular tepal limbs typical of the species, and narrower, navy blue 'beetle spots', much larger style branches and protruding style crests, and its lower leaf surfaces are densely pubescent (Goldblatt, 1986). Both these taxa occur within the Elandsberg Private Nature reserve near Hermon.

Moraea tulbaghensis commences growth in late autumn once sufficient rains have fallen. Rapid vegetative growth continues throughout winter and flowering begins in early September (2 weeks earlier in cultivation). Flowering is prolific in the spring season following bush fires of the immediately preceding summer, but the species is not dependent on fire for flowering to occur. Although each flower lasts just 3 days, a succession is produced over a 2- to 3-week period. The ripe seed capsules split longitudinally from the apex downwards and remain attached until all the seeds have been released in gusts of wind.

In the first pollination study of 'peacock' moraeas it was found that *M. tulbaghensis* is pollinated by hopliine beetles (Scarabaeidae) that are attracted to the contrasting iridescent dark green or blue markings located near the base of the large outer tepals; the typical forms of this species were found to be pollinated primarily by *Peritrichia abdominalis*, whereas the plants previously classified as *M. neopavonia* were pollinated primarily by a new species of *Monochelus* (Steiner, 1998), later named *M. steineri*. Other pollinators recorded for this species are *Lepithrix ornatella* (Steiner, 1998) and *Anisochelus inornatus*, *Apis mellifera*, *Argoplia glaberrimus* and *Heterochelus detritus* (Goldblatt *et al.*, 2006). I have often observed honey bee workers (*Apis mellifera*) gathering pollen and evidently effecting pollination of *M. tulbaghensis* in open bulb beds in the Kirstenbosch Nursery.

CULTIVATION. Despite its ease of culture and spectacular blooms, *Moraea tulbaghensis* is rarely grown, other than by specialist collectors. This is surprising, for in ideal conditions the corms are long-lasting (up to 15 years), flower reliably every year and set abundant seed with which to replenish stocks following hand-pollination. I have been growing this species in the Kirstenbosch Bulb Nursery for more than 25 years and have found the plants best suited for cultivation purposes to be the large-flowered, tall-growing forms with navy-blue nectar

Fig. 1. *Moraea tulbaghensis* with attendant beetles near Gouda. Photograph: Graham Duncan.

Fig. 2. A red form of *Moraea tulbaghensis* in the Elandsberg Private Nature Reserve near Hermon, south-western Cape. Photograph: Graham Duncan.

guides and heavily dark-spotted tepal claws, previously classified as *M. neopavonia,* as they are more floriferous compared with the typical forms, however, they need better drainage than the typical forms (Du Plessis & Duncan, 1989). The tall-growing forms are suited to deep bulb beds or containers with a diameter of 30–35 cm, whereas the smaller, typical forms perform well in deep, 25 cm diam. pots. The plants are half-hardy, and able to withstand temperatures down to freezing for short periods (Duncan, 2010). They cannot abide high humidity and need very dry summers. An aspect receiving full morning sun, or bright light for as much of the day as possible, is required, and the plants are most suitably grown under cover, such as in the cool greenhouse in cold climates or on a sunny patio in temperate parts, to prevent rain and insect damage to the delicate outer tepals. Tall-growing forms may need to be carefully staked in windy areas.

Plant the corms in autumn at a depth of 3 cm in a freely draining medium of equal parts of course river sand and finely sifted, acid compost, with the corms resting in a layer of pure river sand to discourage attack by soil-born fungi. After an initial heavy drench in mid-autumn, wait for the leaf shoots to appear, then apply a twice-weekly drench throughout winter and until the end of spring, at which time the leaves naturally turn brown as temperatures rise. The dormant corms can be stored in their pots in a cool dry place for the summer.

This species is not suited to general garden cultivation as the corms cannot abide indiscriminate watering in summer, but dedicated rock garden pockets that have been lined with wire mesh to exclude mole rats can be used, and judicious weeding by careful cutting just below soil level is necessary to prevent the plants becoming smothered. In susceptible areas, the corms will also be taken by porcupines, or scratched out and consumed by guinea fowl (Duncan, 2009). Cross-pollination by hand amongst different clones is essential in order to obtain pure seeds and have seedlings coming-on in case of loss of mature corms. Plentiful bright orange pollen is produced, and seed set is usually excellent, often producing more than 100 seeds per capsule. Isolation of the plants from other moraeas prior to opening is recommended as this species readily forms hybrids with other ‘peacock’ moraeas, including *M. aristata* and *M. villosa*, when grown in close proximity.

Moraea tulbaghensis is easily raised from fresh seeds harvested from the immediately preceding flowering season. Sow the seeds under cover in bright light in mid- to late autumn in deep seed trays, pots or deep seed beds, once cool weather has definitely set in, at a depth of 3–4 mm, and sow thinly to prevent overcrowding and reduce the likelihood of loss to damping-off fungi. Germination takes place within 4–6 weeks and seedlings should be kept moist by watering with a fine rose-cap. Seedlings should be left undisturbed for two growing seasons before lifting and planting into permanent containers at the beginning of their third winter growing season. Well-grown corms should flower for the first time during the third year. Seed viability decreases markedly if stored at room temperature for more than 6 months, but can be maintained for a number of years and retain viability when stored dry at low temperature, such as in the vegetable compartment of a fridge. This species can also be propagated by removal of corm offsets that sometimes develop at the base of the mother corm, in autumn, just before active growth begins.

The flower buds and developing fruits are sometimes attacked by aphids, and the leaf lower surfaces are subject to infestation by red spider mites towards the end of the flowering season.

Moraea tulbaghensis L.Bolus, South African Gardening and Country Life 22:276 (1932). Type: South Africa, Western Cape, Saron, near Tulbagh, *L. Bolus s.n.* (BOL! sub. 16738).

Moraea neopavonia R. Foster, Contributions to the Gray Herbarium 165: 107 (1947), nom. nov. pro *Moraea pavonia* (L.f.) Ker Gawl., nom. illeg. *Iris pavonia* L.f., Supplementum plantarum: 98 (1782). Type: South Africa, Cape, Swartland hills, *Thunberg s.n.* (UPS, Herbarium Thunberg 1148A, lectotype, designated by Goldblatt, 1976).

DESCRIPTION. *Deciduous, winter-growing geophyte* 250–600 high. *Corm* globose, 12–15 mm in diam., solitary, white, solitary, surrounded by fairly hard, light brown outer tunics, offset-forming in cultivation. *Leaf* 1, linear, 300–620 × 3–6 mm, basal, canaliculate, bright green, lower surface pubescent, midrib prominent on lower surface, apex dry and brown, acute. *Stem* erect, minutely pubescent, bright green; stem nodes 2, prominent, sheathing stem bracts erect, 55–70 mm long, bright green, apices attenuate, light brown; outer and inner spathe bracts bright green, 40–65 mm long, apices light brown, attenuate, overlapping. *Inflorescence* a rhipidium, one- or rarely two-branched, producing one to three flowers at staggered intervals. *Flowers* cupped to spreading, light to bright orange, brick-red or rarely yellow or white; three outer tepals broadly lanceolate or more or less spathulate, 25–30 × 16–30 mm, spreading or slightly ascending, margins sometimes undulate, iridescent spots prominent, peacock-green or navy-blue outlined in black; tepal claws 10–12 × 6–10 mm, glabrous or minutely bearded, orange, rarely yellow or white, black-spotted; three inner tepals linear to narrowly lanceolate or tricuspidate, 14–18 mm long, central lobe 1–5 mm wide, two lateral lobes absent or obtuse. *Filaments* 4–6 mm long, fused below, uppermost portion free, brownish; anthers linear, 7–12 mm long, pollen light to bright orange or reddish when ripe. *Ovary* oblong, 10–15 mm long, light green, protruding well above spathe bracts; style branches suberect, 6–8 × 2–3 mm, light to bright orange or white, style crests triangular, 2 mm long, inconspicuous. *Capsule* cylindrical, 20–30 × 5–6 mm. *Seeds* angular, 1 × 1 mm, light brown. *Chromosome number*: 2n = 12 (Goldblatt, 1976).

DISTRIBUTION. Confined to a narrow range from Piketberg to Wellington in the western and south-western part of the Western Cape.

HABITAT. In colonies on stony clay flats and lower hill slopes amongst grasses and low bushes, in full sun.

FLOWERING TIME. September to October, with a peak in mid-September.

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720. MORAEA VILLOSA
Iridaceae

Graham Duncan

Summary. The Western Cape petaloid geophyte *Moraea villosa* (Ker Gawl.) Ker Gawl. is described and details of its history, biology, cultivation and propagation are given, accompanied by a watercolour plate and habitat photographs.

Moraea villosa is certainly the most often cultivated of the ‘peacock’ moraeas, and is widely regarded as the flagship species of this alliance, although the striking white- and blue-flowered *M. aristata* (D. Delaroche) Asch. & Graebn (t. 719 above), has equally striking iridescent spots and was known to science at least 15 years earlier. *M. villosa* was initially described by C. P. Thunberg as a variety of *Iris tricuspis* L.*f*. (now *Moraea tricuspidata* (L.f.) G. J. Lewis), as var. *corolla-purpurea* Thunb., in his *Dissertatio de Iride* (Thunberg, 1782). It was the English botanist John Bellenden Ker Gawler (±1764–1842) who was the first to recognize it as an independent species, though he also originally described it as an *Iris*, *I. villosa* Ker Gawl. in *Curtis's Botanical Magazine* (Ker Gawler, 1802), but later transferred it to *Moraea* in the *Annals of Botany* (König & Sims), in 1805 (Goldblatt, 1986). An expert on the Iridaceae, Ker Gawler is well remembered for his *Iridearum Genera* published in Brussels in 1827, and he was the Editor of *Edwards's Botanical Register* from 1815 to 1824. His specific epithet *villosa* is descriptive of the villous or pubescent lower leaf surfaces and stems.

Moraea villosa subsp. *elandsmontana* Goldblatt was discovered by Fay Anderson in 1979 at the foot of the Elandsberg Mountains within the Elandsberg Private Nature Reserve near Hermon, southwest of Tulbagh, (Fig. 2). It was described in the *Annals of the Missouri Botanical Garden* (Goldblatt, 1982) and illustrated by Fay Anderson on plate 83b of *The Moraeas of Southern Africa* (Goldblatt, 1986). The only other published painting of it is that by Elise Bodley, reproduced on plate 26 of *Bulbous Plants of Southern Africa* (Du Plessis & Duncan, 1989) from material collected by the Cape nature conservation officer Chris Burgers in 1981, and cultivated in the bulb nursery at Kirstenbosch.

Moraea villosa is closely allied to the orange-, red- or rarely white-flowered *M. tulbaghensis* L.Bolus, and comprises two subspecies, subsp.

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villosa and subsp. *elandsmontana*. Placed within subgenus *Vieusseuxia* and section *Vieusseuxia*, *M. villosa* has relatively long-lasting flowers that remain fresh for 3 days, and is distinctive in its large, almost round outer tepals with a prominent central yellow or orange pubescent nectar guide, surrounded by various crescent-shaped dark colour combinations, often outlined in white, yellow or orange (Goldblatt, 1986).

The subsp. *villosa* is known colloquially as 'UILTJIE', an Afrikaans word meaning 'small owl', alluding to the prominent owl-like 'eyes' at the base of the outer tepal limbs (Fig. 1).

Moraea villosa subsp. *villosa* has the widest distribution of all the peacock moraeas, occurring from just north of Piketberg on the west coast, to Ceres in the Warm Bokkeveld and south to Gordon's Bay, east of Cape Town. The two most important vegetation types it frequents are Swartland- and Breede Shale Renosterveld, both highly threatened, of which the former is critically endangered, 90% of it having been transformed, with very little of the remaining area conserved statutorily (Mucina & Rutherford, 2006).

The species is rather variable in outer tepal size and colouring, and in degree of leaf hairiness. Most forms of subsp. *villosa* are light to deep mauve-flowered with blue 'beetle spots', but tepal colour also ranges in shades of cream, pink, blue and purple, and spots of certain forms vary in shades of turquoise or black, sometimes outlined in white, brown, yellow or orange. A beautiful mauve form from Malmesbury has the largest black spots of all the colour variants, and a large blue-flowered form from just north of Piketberg has almost hairless leaves, compared with those from the Paardeberg near Paarl that are comparatively hairy. The subsp. *elandsmontana* is confined to a single site at the base of the Elandsberg Mountains and has bright orange or very rarely, white or bright yellow tepals with relatively narrow, crescent-shaped, navy blue beetle spots. Apart from colour differences and geographic isolation, the subsp. *elandsmontana* differs in being a diploid ($2n = 12$), in contrast to subsp. *villosa* that is tetraploid ($2n = 24$).

Moraea villosa is pollinated by beetles, almost exclusively by hopliine scarab beetles of the family Scarabaeidae, which are attracted to the dark 'beetle spots' at the base of the outer tepal limbs. The beetles visit the flowers for pollen and mating; pollinating beetle species recorded

Plate 720 *Moraea villosa* GEORITA HARRIOTT

Fig. 1. A mauve form of *Moraea villosa* subsp. *villosa* in habitat south of Tulbagh. Photograph: Graham Duncan.

thus far include *Anisochelus inornatus*, *Anisonyx ditus*, *A. ursus, Lepithrix lebisii*, *L. ornatella* and *Peritrichia rufotibialis* (Steiner, 1998; Goldblatt *et al*., 2006).

Fig. 2. *Moraea villosa* subsp. *elandsmontana* in habitat, Elandsberg Private Nature Reserve near Hermon, southwestern Cape. Photograph: Graham Duncan.

Moraea villosa favours stony, fertile shale soils in full sun on flats and lower hill slopes. The plants grow in small to large colonies amongst low scrubby growth, often in association with other petaloid geophytes. At a site south of Tulbagh, a bluish-mauve form grows together with a multitude of other spring-flowering bulbous, cormous and tuberous plants including the wine-red *Babiana villosa* (Aiton) Ker Gawl. and *Geissorhiza erosa* (Salisb.) R. C.Foster, the light blue *Lachenalia unifolia* Jacq. and the bright pink orchid, *Satyrium erectum* Sw.

Agricultural expansion for winter cereal crops, vineyards, orchards, as well as the devastating effects of housing development, road construction, eutrophication and the spread of alien plants, have decimated more than 80% of the habitat of subsp. *villosa*; it is probably known from fewer than 20 sites today and has a conservation status of Vulnerable (Raimondo & Goldblatt, 2009). Although the subsp. *elandsmontana* is protected within the Elandsberg Private Nature Reserve, it is known from only one population, and it too qualifies for the Vulnerable threat category (Goldblatt & Raimondo, 2009).

CULTIVATION. The cultivation of *Moraea villosa* presents no difficulty in suitable conditions and it is grown in the same manner as *M. aristata*, *M. loubseri* and *M. tulbaghensis*. Its corms are not quite as resilient as those of *M. aristata* but it has the same requirements of full sun or bright light, deep containers 25–30 cm in diam., a well drained medium containing equal parts of silica sand or river sand and finely sifted, well decomposed organic matter, heavy drenching throughout the winter growing period and spring flowering period, and a completely dry summer rest. Where temperatures do not fall below freezing for extended periods in winter, it can be grown in outdoor bulb beds or dedicated rock garden pockets that are kept dry in summer, provided they have been securely lined with wire mesh to exclude mole rats, but in cold climates it requires the protection of the cool greenhouse (Duncan, 2010). One of the most outstanding forms for cultivation is a deep mauve-flowered form of subsp. *villosa* from Malmesbury, now sadly almost extinct there due to housing development, which has especially large black 'eyes', illustrated by Barbara Jeppe on plate 50a of *Spring and Winter Flowering Bulbs of the Cape* (Jeppe & Duncan, 1989). Its corms are long-lived (up to 10 years or more in ideal conditions) and with sufficuent moisture at flowering time, is in bloom for at least 3 weeks from early to late September. Subsp. *elandsmontana*, a plant whose beauty defies description, I have found to be less vigorous than the typical subspecies, less inclined to reproduce vegetatively and requiring more frequent repotting to encourage flowering every year. When growing *M. villosa* in close proximity to other peacock moraeas, it is necessary to isolate the plants and cross-pollinate by hand, as hybrids readily occur between this species, *M. aristata* and *M. loubseri* where insects have free access.

Germination of fresh seeds harvested from the immediately preceding season is excellent and takes place within 5 weeks. They are best sown at a depth of 3–4 mm in deep pots or seed beds, and allowed to remain undisturbed for a second season before planting into permanent positions at the beginning of their third season, during which flowering can be expected for the first time. Like those of *Moraea aristata*, the corms of *M. villosa* produce cormlets at the tips of subterranean stolons and these are easliy removed once large enough and potted-up in early autumn. The hairy leaves and stems of *M. villosa* are much less prone to aphid attack than species with smooth surfaces, but the flower buds and developing fruits are subject to aphid infestation, and the leaf undersides sometimes fall prey to attack by red spider mites as temperatures rise in late spring. Mole rats, Namaqua rock mice and Cape porcupines are partial to the corms, and an insufficiently dry summer rest phase can result in fungal rotting of the corms.

Moraea villosa (Ker Gawl.) Ker Gawl., Annals of Botany (König & Sims) 1: 240 (1805).

Iris tricuspis L.f. var. *corolla purpurea* Thunberg, Dissertatio de Iride 15 (1782). Type: South Africa, Cape, precise locality unknown, *Thunberg s.n.* (UPS, Herb. Thunberg), nom. inval.

Iris villosa Ker Gawl., Curtis's Botanical Magazine 16, t. 571 (1802).

Vieusseuxia villosa (Ker Gawl.) Sprengel, Systema Vegetabile 1: 165 (1825). Type: South Africa, Cape, precise locality unknown, figure in Curtis's Botanical Magazine 16, t. 571 (lectotype, designated by Goldblatt, 1986).

Description. *Deciduous, winter-growing geophyte* 130–410 mm high. *Corm* globose, 13–15 mm in diam., solitary, white, forming cormlets at apices of subterranean stolons; outer tunics fairly hard, light brown, apices fasciculate; cataphylls 2, membranous. *Leaf* solitary, linear, 200–550 × 2–4 mm, basal, suberect or spreading, bright green, bifacial, lower surface and margins minutely pubescent. *Stem* erect, minutely pubescent, sometimes 1–2-branched, stem nodes 3, prominent; stem bracts 2, 30–65 mm long, sheathing, apices attenuate, brown; spathe bracts 2, overlapping, apices attenuate, brown, outer bract 25–45 mm long, inner bract 45–70 mm long; pedicel light green below, shading to brown above, 40–62 mm long, mostly obscured by spathe bracts. *Inflorescence* a rhipidium, sometimes 1–2-branched, producing 1–3 flowers per branch at staggered intervals. *Flowers* light to deep mauve, purple, pink, orange, rarely white, cream or bright yellow; outer tepals suborbicular, 25–30 × 20–40 mm, spreading, claws suberect, 10–14 × 7–15 mm, upper surface pubescent, nectar guides yellow or orange, with a prominent iridescent light to deep blue, turquoise or black spot, sometimes outlined in white, orange, brown, yellow or orange; inner tepals tricuspidate, 18–28 × mm long, lower portion suberect, firm, free upper central lobe linear, lateral lobes obtuse, 2 × 2 mm, upper surface plain or with purple markings. *Filaments* fused almost to apex, 4–5 mm long, bluish white; anthers 6–7 × 1 mm, linear; pollen maturing to bright orange. *Ovary* cylindrical, 10–15 × 2–3 mm, protruding above spathe bracts, light green or brown; style branches suberect, 5–8 × 4–6 mm, white, light orange or rarely yellow, crests white or orange; stigmas recurved, 1 × 1 mm. *Capsule* cylindrical, 18–30 × 3–6 mm. *Seeds* angular, 1 × 1 mm, light brown. *Chromosome number*: 2n = 24 (subsp. *villosa*); 2n = 12 (subsp. *elandsmontana*) (Goldblatt, 1982).

DISTRIBUTION. North of Piketberg to Ceres and Gordon's Bay, in the western and southwestern part of the Western Cape.

HABITAT. Lower hill slopes and flats in stony clay soil amongst low scrub, in full sun.

FLOWERING TIME. Late August to late September, with a peak in mid-September.

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MORAEA LOUBSERI
Iridaceae

Graham Duncan

Summary. The history, ecology, conservation status, cultivation and propagation requirements of the highly threatened and extremely localised Western Cape endemic irid *Moraea loubseri* Goldblatt are discussed, accompanied by a botanical description, photographs in cultivation.

Moraea loubseri attracted a lot of attention at the time of its discovery recently near the resort town of Langebaan on the Cape west coast, for two reasons. Firstly, its exceptionally attractive violet-mauve outer tepals, contrasted with a blue iridescent nectar guide and very unusual large black beard over the tepal bases and claws captured the imagination of growers of indigenous Cape geophytes, and secondly its apparent endemism to a single, very localized locality, a striking feature of numerous species within the Cape geophyte flora, stimulated the interest of conservationists. Its home was a granite outcrop that was being extensively quarried for ballast for use in the construction of a new iron ore harbour terminal in adjacent Saldanha Bay. The plant was found in 1973 on a granite outcrop named Olifants Kop (literally translated to 'elephant's head') by an experienced grower of Cape geophytic species, Johan Loubser, and several years later it was named in his honour in the South African botanical magazine *The Flowering Plants of Africa*, accompanied by a watercolour painting by Fay Anderson (Goldblatt, 1977).

Despite searches of surrounding granite outcrops, no further populations were encountered, and up until the present this has continued to be the case. Although the relevant authorities on whose land the plants occur were alerted to its precarious position, robust measures to fence off the area and protect the remaining individuals in a small nature reserve, did not come to fruition. Fortunately, plants were initially cultivated by Johan Loubser and subsequently, corms and seeds were donated to the bulb collection in the nursery at Kirstenbosch. Here the plants have thrived and multiplied to the extent that in 1980, I was able to make 135 packets of surplus seeds available for distribution to members of the Botanical Society of South Africa, and seeds were and subsequently distributed to members on numerous

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occasions (Duncan, 1981). *M. loubseri* is now well established in bulb collections in this country and abroad, including Australia, France, New Zealand, the UK and the USA, and seeds harvested from hand-pollinated plants grown at Kirstenbosch are lodged in long-term cold storage at the Millenium Seed Bank at Wakehurst Place in Sussex.

Moraea loubseri belongs to the group of species popularly known as 'peacock' moraeas that form part of subgenus *Vieusseuxia,* whose members have relatively long-lasting blooms (3 days) with brightly coloured, large outer tepals with prominent iridescent spots. The species is thought to be most closely allied with *M. villosa* (Ker Gawl.) Ker Gawl. that has similarly shaped inner tepals and a similar pubescent stem and leaf. *M. loubseri* has such distinctive flowers that it would be difficult to confuse it with any other, (Figs 1 & 2); the only one that comes close to it is another striking bluish-mauve species from the Saldanha Bay area, to which *M. loubseri* is undoubtedly related, the endangered *M. calcicola* Goldblatt that was also discovered by Johan Loubser, in 1976, just 3 years after his discovery of *M. loubseri. M. calcicola* is also limited to a single known population and is endemic to rocky limestone deposits on a large granite outcrop just above the town of Saldanha, a short distance to the northwest of Langebaan. It has similar black-bearded tepal claws and outer tepal bases, and pubescent leaf lower surfaces, but differs mainly in its much larger, orbicular outer tepals and taller stature, and it flowers later in the season, from mid-to late September (Goldblatt, 1986).

Actual pollinator sightings for *Moraea loubseri* have not been recorded, and it seems unlikely they ever will be, unless sufficient numbers of plants make a re-appearance or we are able to re-introduce plants to the original site. However, it can safely be assumed that hopliine beetles (family Scarabaeidae) are the probable pollinators, in accordance with other members of subgenus *Vieusseuxia* that possess prominent beetle marks and are pollinated by these insects (Goldblatt *et al.*, 2006).

Moraea loubseri is endemic to sandy, granite-derived soil of the Saldanha Granite Strandveld vegetation type that is only found on the Cape west coast stretching from St Helena Bay in the north to Langebaan in the south, and its adjacent peninsula. The vegetation is always associated with granite domes and comprises small to medium-sized scrubby growth, interspersed with a rich succulent

Fig. 1. *Moraea loubseri* in cultivation at Kirstenbosch. Photograph: Graham Duncan.

Fig. 2. Detail of *Moraea loubseri* in cultivation at Kirstenbosch. Photograph: Graham Duncan.

and geophyte flora (Mucina & Rutherford, 2006). Probably the most critically endangered of all cormous plants in South Africa, up until very recently, the possibility existed that *M. loubseri* may have become extinct in the wild. In 1980 it was declared extinct in the South African National Scientific Programmes Report no. 45, but in the spring of 1982, Johan Loubser revisited the original site and reported some 200 plants in flower. It would appear that certain visitors to the site may not have known precisely where the plants grew and not finding any in flower, considered it extinct (Geary-Cooke, 1983). It seems mysterious that since 1982, almost all remaining individuals have been lost, and in recent times, fewer than five plants were recorded in 1995 and 2002, and no specimens at all were located in the wild between 2005 and 2010. Consequently, the species was judged to have a conservation status of Critically Endangered, Possibly Extinct

(Snijman *et al.*, 2009). Nevertheless, it is not an infrequent occurrence for 'extinct' species in the Cape Flora to suddenly reappear, and hope still remained that it may make a comeback, and indeed, in early September 2011, amid great excitement, two plants were discovered by the botanist Rupert Koopman at the original site.

CULTIVATION. Like the critically endangered *Moraea aristata*, the position of *M. loubseri* is somewhat paradoxical in that despite its extreme rarity in the wild, it responds very well to cultivation, flowering reliably every year provided certain requirements are met. The plants perform admirably in deep pots with a diameter of 25 cm and can be grown in a variety of well drained acid or alkaline media. In the Kirstenbosch Bulb Nursery I grow it in a mixture of equal parts of course industrial (silica) sand and finely milled bark, with a 3 cm layer of well-rotted, acid compost placed at the base of the container over the drainage crocks. Mature corms are planted 2 cm deep and in order to reduce the possibility of fungal infection, are placed within a layer of pure sand. An initial heavy drench is provided in mid-autumn, followed by twice-weekly applications once the leaves appear and throughout the winter growing period. It is especially important to maintain sufficient moisture during flower bud formation to prevent their abortion and the plants entering dormancy prematurely. Similarly, the plants require sufficient moisture during the flowering and fruiting periods to perform optimally.

Although the corms are fairly long-lived, lasting about 8–10 years under ideal conditions, in order to maintain this species in cultivation over the long term in collections, it is necessary to isolate and cross-pollinate flowers by hand in order to have a stock of developing young plants coming-on, in case of sudden loss of adult plants. Cross-pollinating *M. loubseri* flowers is easily accomplished. Pollen can be collected by dabbing a water paintbrush over the ripe anthers, which are located directly beneath the style branches. Pollen is ready for collection once it has turned bright orange and become somewhat sticky, then, moving to a flower of a different clone, gently brushed over the two stigma 'flaps' situated just above the top of each anther. Seed sets readily after successful fertilisation and an abundance can be obtained from a single capsule. *M. loubseri* is half-hardy and able to withstand temperatures down to 0°C for short periods, but in cold winter climates it needs to be grown in the cool greenhouse (Duncan, 2010). When maintaining a large bulb collection, it is important to harvest the ripe capsules in time, just after they have started to split, as the seeds are released in gusts of wind and readily colonise adjacent pots (Duncan, 1997). Once the leaves start turning yellow in early summer, watering must cease until the following autumn.

Moraea loubseri is not suited to general garden cultivation owing to its need for a very dry summer dormant phase, and due to its corms falling prey to mole rats and porcupines. However, in areas not plagued by porcupines, it can be grown in dedicated rock garden pockets that are kept dry in summer, and which have been securely lined with wire mesh to exclude mole rats.

Fresh seeds germinate readily within 3 weeks and in ideal conditions, this species can flower in its second season of growth (Duncan, 1981). More usually though, initial flowering occurs in the third spring season. Excellent viability of fresh seeds is maintained when stored at room temperature for 6 months following harvesting and sowing in the immediately ensuing autumn, but viability decreases markedly thereafter. However, long-term storage of seeds is excellent at 6–7°C, and this can easily be achieved by the home-grower using the vegetable compartment of a fridge. The leaves, stems, flower buds and developing capsules are very susceptible to attack by aphids, and the leaf undersides to red spider mite infestation as temperatures rise markedly in spring. The corms are also sometimes subject to attack by mealy bugs.

Moraea loubseri Goldblatt, Flowering Plants of Africa 44: t. 1724 (1977). Type: South Africa, Cape, Olifants Kop at Langebaan, *Goldblatt 2076* (MO, holotype; K, NBG, PRE, S, isotypes).

DESCRIPTION. *Deciduous, winter-growing geophyte* 150–260 mm high. *Corm* globose, 8–12 mm in diam., white, outer tunics fibrous, moderately firm, light brown, offset-forming. *Leaf* 1, linear, 300–600 × 3–5 mm, basal, canaliculate, bright green, upper surface glabrous, lower surface minutely pubescent, midrib prominent on lower surface, apex acute. *Stem* erect, minutely pubescent, bright green; stem nodes 2, prominent; sheathing stem bracts erect, 50–60 mm long, bright green, apices attenuate, light brown; outer and inner spathe bracts bright green, 3–5 mm long, apices light brown, attenuate, overlapping. *Inflorescence* a rhipidium, sometimes 1-branched, producing 1–3 flowers at staggered intervals. *Flowers* light to deep violet-mauve; three outer tepals more or less spathulate, 22–30 × 15–20 mm, spreading or slightly to strongly reflexed, apices apiculate, upper surface light to deep violet-mauve with deeper violet midrib, with a small triangular, navy blue iridescent spot in middle near base, just above black beard, lower surface light violet-mauve, margins slightly undulate; tepal claws 5 × 5 mm, upper surface heavily bearded with black, lower surface light green; three inner tepals tricuspidate, 15–20 mm long, central lobe linear, light violet-mauve, deep purple at base, spreading; two lateral lobes light violet-mauve above, fused lower portion light blue and violet-spotted. *Filaments* 4–5 mm long, light blue, fused below; anthers three, linear, 5–6 mm long; pollen bright orange when ripe. *Ovary* oblong, 8–10 mm long, protruding above spathe bracts, light green; style branches spreading to suberect, 10 × 3 mm, midribs dull blue, margins hyaline; style crests 2 mm long, brownish mauve. *Capsule* cylindrical, 15–20 × 3–5 mm. *Seeds* angular, 1 × 1 mm, light brown. *Chromosome number*: 2n = 12 (Goldblatt, 1986).

DISTRIBUTION. Confined to a single site near Langebaan on the Cape west coast.

HABITAT. Amongst low scrubby growth in sandy, granite-derived soil of a granite outcrop, in full sun.

FLOWERING PERIOD. August to early September, with a peak from mid- to late August.

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721. MASSONIA BIFOLIA

Hyacinthaceae

John Manning, Peter Goldblatt and Rachel Saunders

Summary. The history, ecology, pollination biology and distribution of *Massonia bifolia* (Jacq.) J.C. Manning & Goldblatt. (= *Whiteheadia bifolia* (Jacq.) Baker) are given, and its position in the tribe Massonieae is briefly discussed. Cultivation notes are provided.

This curious bulb has fascinated botanists and botanical artists for over ~~3~~ centuries but has only recently divulged the secret of its intriguing appearance. Restricted to the semi-arid, winter-rainfall region along the South African west coast, *Massonia bifolia* is scarcely known in cultivation beyond specialist collections but is instantly recognized by the pair of prostrate leaves flanking a squat, leafy spike of greenish flowers surmounted by a crown or coma of sterile floral bracts. The soft, semisucculent leaves are unusually fragile and readily damaged, reputedly even by raindrops (Obermeyer, 1965). Its distinctive inflorescence, with its sweeping, leafy eaves, suggested the common name PAGODA LILY (Manning *et al.*, 2000).

Initially described as *Eucomis bifolia*, it was one of dozens of Cape bulbs that were first illustrated in Nikolaus von Jacquin's monumental florilegium, *Icones Plantarum Rariorum* (Jacquin, 1781–1793). The coloured engravings in this, like those in his other works, were based largely on plants from the Imperial Gardens at Schönbrun or from the University Botanic Garden (Rix, 1989). Most of the South African material figured in these volumes was collected by the Schönbrun gardeners Georg Scholl and Franz Boos, despatched to the Cape of Good Hope in 1786 at the request of Jacquin himself. Once there, they undertook several collecting trips in the region, initially in the company of the Scottish gardener Francis Masson, who was there at the behest of Sir Joseph Banks on a similar errand on behalf of Kew. Boos, who docked in Trieste on June 17, 1788 laden with natural history specimens gathered in the Cape and the Indian Ocean islands of Mauritius and Reunion over the preceeding 2 years, was handsomely rewarded for his efforts by Emperor Josef II. Scholl was detained at the Cape for a further thirteen years, in no small measure by the low esteem in which the Dutch held the Holy Roman Emperor, before

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Plate 721 *Massonia bifolia* LUCY SMITH

eventually making his way back to Vienna in 1799 to claim his reward for service to the Empire. Although their itinerary is not known, some of their collections make it clear that Boos and Scholl (or more likely Scholl alone) travelled well north of Cape Town into Namaqualand.

The extraordinary success of the efforts of Boos, Scholl and Masson fuelled the passion for Cape plants that was sweeping the botanical and horticultural fraternities of Europe at the turn of the 18th century, (Manning *et al.*, 2002). Among those who succumbed to its allure was the wealthy London merchant George Hibbert, one of the 'opulent commercial men' and 'great encouragers of exotic botany' of the time, who has amassed a most impressive 'collection of heaths, Banksias and other Cape and Botany-Bay [sic.] plants' (Desmond, 1994). Hibbert engaged James Niven, another of the indefatigable Scottish gardeners that were active in Georgian Britain, to travel to the Cape as his resident collector between 1798 and 1803. Niven's evident success on behalf of his English patron prompted the Empress Josephine to engage him on his return, sending him straight back to repeat his endeavours on France's behalf! It was Hibbert's greenhouses that furnished the plant that was illustrated and described by Henry Andrews (1804) as the new species *Melanthiun massoniifolium* (a later synonym of *Massonia bifolia*) and it is certain that it was Niven who collected it. It is almost as certain that Hibbert shared his material with E. John Alexander Woodford, another London plant enthusiast, as Woodford was able to provide William Curtis with a flowering specimen for illustration a year later (Ker-Gawler, 1805).

It appears that Niven travelled only as far north as Clanwilliam during his commission for Hibbert but this is just far enough to have enabled him to encounter the species at its southern limit in the northern Cedarberg Mountains. Fifty years were to pass before the species was seen in the wild again, this time around the mission station at Modderfontein west of Springbok in northern Namaqualand, where the resident Anglican clergyman Rev. Henry Whitehead found it in 1855–1856. His specimen formed the basis for *Whiteheadia latifolia*, described by colonial botanist William Harvey (1868), who had overlooked its earlier introduction in Vienna. Although struck, like Jacquin before him, by the similarity of the curious mop of sterile bracts capping the floral axis to that in the genus *Eucomis*, Harvey was led by the difference in habit (notably the pair of leaves and spike-like inflorescence), hooked style, and papery, winged capsules, to treat the species in a separate genus in honor of its putative discoverer. The association between Harvey's genus and Jacquin's earlier epithet was established by the Kew botanist J. G. Baker (1873), and the species was subsequently known under the name *Whiteheadia bifolia* until recently, when it was transferred to the genus *Massonia* (Manning *et al.*, 2004).

Winter rainfall southern Africa is the centre of diversity for the tribe Massonieae, which includes 9 genera and ± 200 species of these often attractive bulbous plants. Most of the genera are small, with the great majority of the species (±120 spp.) included in *Lachenalia* J. Jacq. ex Murray. Among the remainder, only *Ledebouria* Roth (±50 spp.) comprises more than a handful of species. Generic circumscriptions in Hyacinthaceae have hinged in the past on often subtle floral differences, with significant disagreement among botanists on generic boundaries. The introduction of DNA sequence data has provided a welcome source of additional information, and a consensus on the evolutionary relationships among the species is now emerging. This suggests that several of the traditional species associations were erroneously founded on morphological convergences, necessitating a complete review of the characters used to define genera. The recent and unexpected discovery of two species of uncertain generic affinity from a remote valley in arid southern Namibia (Müller-Doblies & Müller-Doblies, 1997) has further complicated matters. Until this discovery, *Whiteheadia* Harv., with just a single species, had been separated by its leafy, spike-like inflorescence topped by a coma of large bracts from the allied genus *Massonia* Houtt., in which the inflorescence is corymbose and lacking a coma. The description of a second species of *Whiteheadia*, *W. etesionamibensis* U.Müll.-Doblies& D.Müll.-Doblies, with rather smaller bracts subtending the flowers, was therefore of particular interest. DNA data indicate that this species falls between *Whiteheadia* and *Massonia* rather than grouping immediately with *Whiteheadia*, providing grounds for concluding that it shared a recent common ancestor with *Massonia.* Available evidence, therefore, suggests that it occupies an evolutionary position intermediate between the two genera, as a result of which we elected to treat *Massonia* rather more broadly than before to include *Whiteheadia*, rather than embrace the alternative solution of describing an additional monotypic genus for *W. etesionamibensis* (Manning

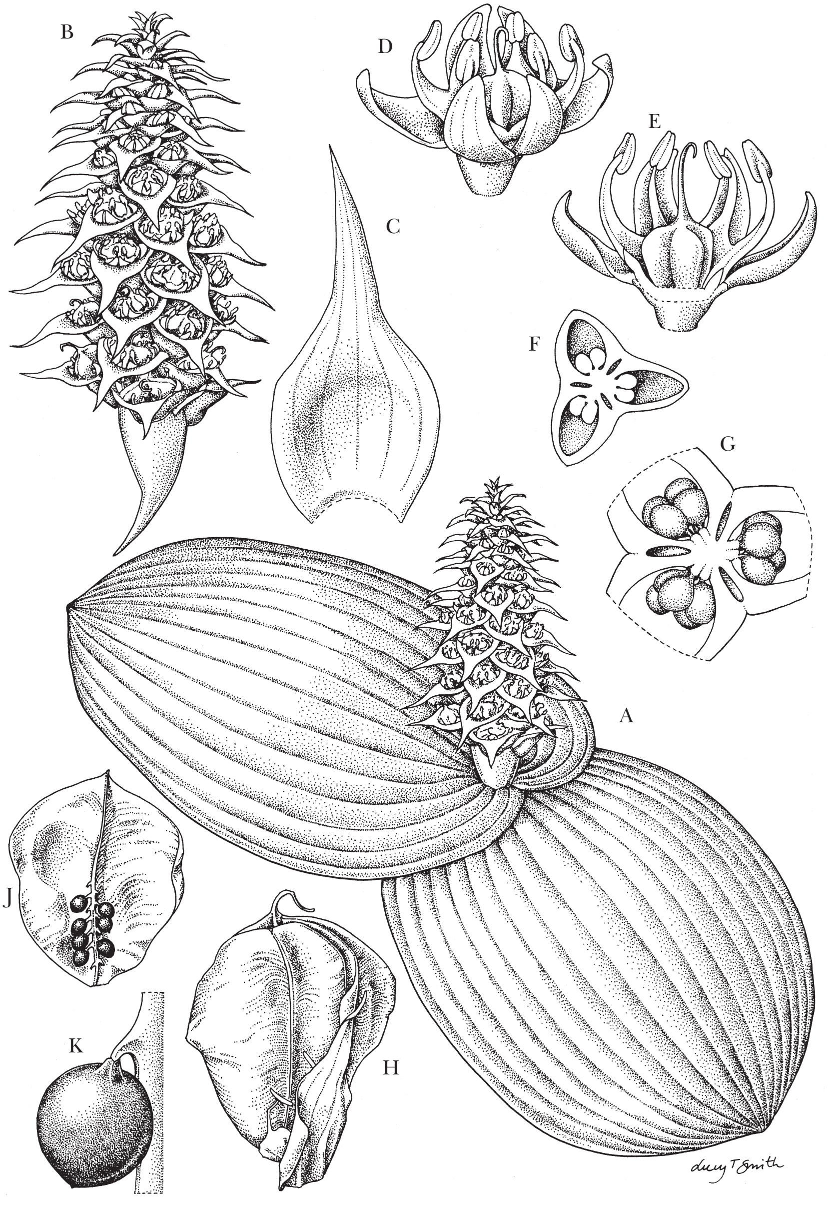

Fig. 1. **Massonia bifolia**. A, whole plant, × ⅓; B, inflorescence, × ½; C, bract, × 1.5; D, flower, × 1.5; E, flower with 2 perianth segments and stamens removed, × 1.5; F, t.s. ovary, × 3; G, t.s. ovary, showing immature ovules, × 6; H, ripe capsule, × 1; J, ripe capsule showing seeds, × 1; K, seed, × 7.Drawn by Lucy Smith from plants grown at Kew.

et al., 2004). In this circumscription, *Massonia* now comprises some 10 species, defined by the membranous outer bulb tunics, pair of prostrate leaves, low-flowering habit a very short or subterranean peduncle, conspicuous floral bracts, basally connate filaments, and papery, three-winged capsules (Manning *et al.*, 2004).

The Cape geophyte flora is distinguished by a prevalence of striking and highly unusual morphological and ecological features, many of them presumably adaptations to the semi-arid environment in which the group has diversified (Manning *et al.*, 2002). Several of these are developed in *Massonia*, including the prostrate leaves, which may play a role in maximising photosynthesis at the low teperatures and low incident angle of sunlight that characterise the winter growing season at these moderate latitudes. Adaptation for dispersal of the seeds by wind is another common ecological characteristic, and the large, persistent bracts and winged, papery capsules in the genus assist in this strategy. Unusual pollination systems are not uncommon among Cape bulbs, and pollination by terrestrial rodents is one of the most interesting of these. It has been demonstrated in several species of *Colchicum* L. and in *Massonia depressa* Houtt. (Johnson *et al.*, 2001), and we postulated that the shallow, sour-smelling flowers of *M. bifolia*, borne close to the grouns, were similarly adapted for this strategy (Manning *et al.*, 2002). This has now been confirmed (Wester *et al.*, 2009; Wester, 2011), and *M. bifolia* joins the small group of Cape bulbs that are adapted to pollination by these small mammals. Other features of this strategy, found in both species of *Massonia* with this pollination system, include firm-textured flowers and the production of viscous, sticky nectar. Pollination of *M. bifolia* in the Cedarberg Mountains is accomplished largely through the activities of Namaqua Rock Mice (*Aethomys namaquensis*) (Order Rodentia: Muridae) but occasional visits by the evolutionary distant Cape Rock Elephant-shrews (*Elephantulus edwardii*) (Order Macroscelidea: Macroscelidideae) have also been recorded.

CULTIVATION. Plants of *Massonia bifolia* break dormancy in autumn, growing and flowering through the winter and spring before re-entering dormancy for the summer. Seeds should be sown in autumn when day temperatures are about 22°C and the nights about 10°C. A day–night temperature fluctuation of ± 12°C is required to break seed dormancy. Sow the seeds in plastic pots in a free-draining soil mix and keep them moist. We recommend four to five parts good quality potting mix, one part coarse grit, one part good quality sand and a small amount of well rotted manure.

Keep the seedlings moist through the winter and spring, and dry them off for the summer. Pots should be kept under glass if necessary – they should not freeze and may require 50% shade in summer. In habitat the plants grow in deep shade in the protection of rocks. After the first or second year of growth, once the bulbs are big enough to handle, pot them up into a larger container, in the same well-drained soil mix. The plants can be fed while in growth, using a fertiliser low in nitrogen.

Massonia bifolia (Jacq.) J. C. Manning & Goldblatt, Edinb. J. Bot. 60: 564 (2004).

Eucomis bifolia Jacq., Collectanea 4: 215 (1791). Type: South Africa, without locality or collector, illustration in Icones Plantarum Rariorum 2: t. 449, lectotype designated by Jessop, Jl. S. Afr. Bot. 42: 433 (1976).

Basilaea bifolia (Jacq.) Poir., Encyc. Suppl. 1: 591 (1811).

Whiteheadia bifolia (Jacq.) Baker, J. Linn. Soc., Bot. 13: 226 (1873).

Melanthium massoniifolium Andr. [as '*massoniaefolium*'], Bot. Rep. 6: t. 368 (1804). South Africa, Cape, without precise locality or collector, 'in the Hibbertian collection' (no specimen located); illustration in Andrews, *The Botanists' Repository* 6: t. 368 (1804), lectotype, here designated.

Whiteheadia latifolia Harv., Gen. S. A. Pl., ed. 2.: 396 (1868). Type: South Africa, [Northern Cape], Namaqualand, Modderfontein, *Whitehouse s.n.* (holotype TCD).

DESCRIPTION. *Bulbous perennial*; bulb subglobose, 2–3 cm diameter; outer tunics papery, pale brown. *Leaves* 2, prostrate, elliptical to suborbicular, 8–22 × 5–17 cm, subsucculent and fragile, pale green, veins impressed, clasping at base. *Inflorescence* a stout, conical spike borne at ground level, 3–11 cm long, the peduncle scarcely protruding, tapering below; floral bracts spreading or apically decurved, broadly ovate, acuminate or attenuate, (15)20–40 × 8–20 mm, concave or cupped, subsucculent, green, persisting in fruit, the uppermost bracts sterile and forming a small or conspicuous coma. *Flowers* subsessile, shallowly campanulate, pale green, sour-scented; pedicel stout, short, up to ± 3 mm long; perianth tube cup-shaped, 4–7 mm long; tepals ascending, ovate, 6–9 × 4–6 mm. *Stamens* adnate to the base of the tepals, whitish; filaments erect-incurved, connate basally for 1–2 mm, free parts awl-shaped and 6–7 mm long; anthers 2.5–3.5 mm long, creamy yellow. *Ovary* obtriangular or obovoid, 3–5 × 3–6 mm, green; style ± arcuate, 4–5 mm long. *Capsule* broadly obovoid-subglobose or obtriangular, three-winged, papery, 1.5–2.5 cm diameter, surrounded at first by persistent, papery perianth. *Seeds* globose, ± 2 mm diameter, glossy black.

Distribution. Western southern Africa, ranging from southern Namibia through the higher-lying parts of northern and central Namaqualand to the northern Cedarberg Mountains near Clanwilliam in South Africa.

Habitat. The species is always found in humic pockets in sheltered rocky sites that are locally moist during the winter growing season and that offer shade and protection from the sun throughout the year.

Flowering time. Winter and early spring (June to August in the southern Hemisphere).

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722. GAZANIA KREBSIANA subsp. ARCTOTIODES

Compositae

Graham Duncan

Summary. The herbaceous perennial *Gazania krebsiana* Less. subsp. *arctotoides* (Less.) Roessler is widespread across South Africa and an outstanding garden ornamental. A description and details of its history, biology, cultivation and propagation are provided, accompanied by a watercolour painting and photograph of subsp. *krebsiana* in habitat.

The genus *Gazania* was established by the German naturalist and botanist Joseph Gaertner (1732–1791) when he described *Gazania rigens* (L.) Gaert. in the second volume of his three-volume work on fruits and seeds, *De Fructibus et Seminibus Plantarum* (Gaertner, 1791). This species has given rise to the largest number of garden cultivars and is now cultivated throughout the world. *Gazania* commemorates Theodorus Gaza, the 15th century translator responsible for the first Latin translations of the botanical works of Theophrastus from the Greek. An alternative theory is that the Greek *gaza* alludes to riches, with reference to the richly coloured ray florets. The German botanist C. F. Lessing described *G. krebsiana*, naming it for G. L. E. Krebs, a German naturalist of Hanover who emigrated to South Africa in 1817 and collected plants for the Natural History Museum in Berlin (Lessing, 1832). The epithet *arctotoides*, originally published for the species *G. arctotoides* Less., refers to the resemblance of the flower heads to those of the genus *Arctotis*.

The genus *Gazania* was revised by William Harvey (1865) in *Flora Capensis*, in which 24 species were recognised, and almost a century later Helmut Roessler reduced this number to 16, and recognised three subspecies within *G. krebsiana*; subsp. *krebsiana*, subsp. *arctotoides* (Less.) Roessler, the subject of this article, and subsp. *serrulata* (DC.) Roessler (1959). An outstanding watercolour painting of *G. krebsiana* subsp. *arctotoides* by Auriol Batten in habitat near Clanwilliam was published in *Flowers of Southern Africa* (Batten, 1986). The number of species has recently increased to 18 with the addition of *G. lanata* Magee & Boatwr. from Robertson in the Western Cape and *G. splendidissima* Mucina, Magee & Boatwr. from the Namaqualand coast (Magee *et al.*, 2011).

The genus *Gazania* is native to southern Africa and southern Tropical Africa. It is widespread across South Africa and concentrated mainly in the winter rainfall western and northwestern parts, and extends to Botswana, Lesotho, Namibia and Swaziland. *Gazania krebsiana* has the widest distribution, occurring in all parts of the subcontinent, and the subsp. *serrulata* extends to Angola and Tanzania.

The morphological differences between the subspecies are not very distinct; the involucres of subsp. *arctotoides* and subsp. *serrulata* differ from the typical subspecies in having more or less obtuse or subacute inner bracts as opposed to acuminate ones in subsp. *krebsiana*, and subsp. *serrulata* differs from subsp. *arctotoides* in having completely undivided leaves, as opposed to those of subsp. *arctotoides* in which the leaves of a plant can all be pinnatifid, or have both completely undivided and pinnatifid leaves (Roessler, 1959). Ray floret colour and basal patterning are extremely variable across this species. The ray florets of subsp. *arctotoides* vary in shades of yellow, orange or dark red and have a dark basal portion in shades of brown or greenish yellow, with a prominent black, iridescent, white or often ocellated basal spot or striation. The ray florets of subsp. *krebsiana* are yellow or orange, and in subsp. *serrulata* they are yellow or white.

Within South Africa, subsp. *krebsiana* (Fig. 1) occurs mainly in the southern half of the country in the Western, Eastern and Northern Cape, Free State, KwaZulu-Natal and Lesotho, the subsp. *serrulata* has the widest distribution, occurring in all provinces of South Africa and in Botswana, Lesotho and Swaziland, and the subsp. *arctotoides* is almost as widespread, but absent from Gauteng, KwaZulu-Natal, Lesotho and Swaziland (Roessler, 1959; Retief, 2003).

The holotype of *Gazania arctotoides* Less. was originally collected at Gamko in the Gamka Karoo by two Germans, Johannes Mund and Louis Maire, sent by the Prussian Government as official plant collectors to the Cape in 1816 from the Berlin Zoological Museum (Gunn & Codd, 1981). This material was either lost or destroyed, and a lectotype was designated by Roessler (1959) from other material collected in the Gamka Karoo of whom the collector, date of collection and precise location are unknown, and is housed in the Swedish Museum of Natural History Department of Phanerogamic Botany in Stockholm.

Within the tribe Arctotideae, *Gazania* is one of about eight genera and 130 species within the subtribe Gorteriinae. *Gazania* and other

Plate 722 *Gazania krebsiana* subsp. *arctotoides* GEORITA HARRIOTT

Fig. 1. *Gazania krebsiana* subsp. *krebsiana* in the Tanqua Karoo. Photograph: Graham Duncan.

members of this subtribe are easily set apart from similar-looking genera in subtribe Arctotidinae in that the flowerhead stalks exude a milky latex when cut (Karis *et al.*, 2009). An investigation into the monophyly of the genera within this tribe and their relationship to one another, using three phylogenetic markers, two from chloroplast DNA (*trn*L-F and *ndh*F) and one from the nuclear genome (ITS), showed that *Gazania* falls within one of three monophyletic groups that comprise this tribe, the *Gazania-Hirpicium-Gorteria* group; the other groups being the *Didelta* group and the *Berkheya-Callumia* group (Funk & Chan, 2008). A phylogeny of *Gazania* was published in 2009, based on a molecular phylogenetic analysis of chloroplast and nuclear DNA sequences, in which all Roessler's species were sampled, with the exception of *G. othonnites* (Thunb.) Less. The results indicated that seven species, *G. caespitosa* Bolus, *G. ciliaris* DC., *G. heterochaeta* DC., *G. jurineifolia* DC., *G. lichtensteinii* Less., *G. schenckii* O.Hoffm. and *G. tenuifolia* Less. warranted specific status, but that eight species, *G. krebsiana*, *G. leiopoda* (DC.) Roessler, *G. linearis* (Thunb.) Druce, *G. maritima* Levyns, *G. pectinata* (Thunb.) Spreng, *G. rigens*, *G. rigida* (Burm.*f*.) Roessler and *G. serrata* DC. did not form clear-cut evolutionary units but constituted a species complex (Howis *et al.*, 2009).

Gazania krebsiana is often confused with the similar-looking *G. pectinata,* but the latter differs in that it is usually an annual, has attenuate inner bracts, much longer scapes and is a mainly coastal species, occurring on sandy flats and lower hill slopes.

Monkey beetles are the major pollinators of gazanias in the winter rainfall region of South Africa, congregating and mating on the central disc florets and feeding on their pollen; the brown monkey beetle, *Pachycnema marginella* often visits *G. krebsiana*. The dark spots at the base of the ray florets have been thought to be the major attractor of monkey beetles by mimicing resting beetles, but one study has indicated that in *G. pectinata*, alighting behaviour of monkey beetles was influenced more by ray floret colour, especially orange florets, than by floret patterning or presence of other beetles (Johnson & Midgley, 2001).

Cultivation. In temperate climates, winter-growing *G. krebsiana* is a very useful perennial for rock garden pockets, as an edging plant to herbaceous borders, for stabilising steep banks or planted in deep window boxes. In cold climates, plants are best treated as summer-growers and plunged, then lifted in autumn before the first frosts and over-wintered in a cool glasshouse. Forms from coastal parts of South Africa are certainly tender but those from inland areas, Lesotho and the Drakensberg should be at least frost hardy.

This species is highly adaptable to different soil types but prefers sharply drained, gravelly soils and full sun to flower well. It is suited to difficult coastal gardens as it is tolerant of salt-laden wind. It is recommended for inter-planting with low-growing geophytes and mesembs, and is an excellent choice as a drought-tolerant groundcover (Brown & Duncan, 2006). Depending on whether plants are treated as winter- or summer-growing, they naturally enter a semi-dormant phase for half the year, shrivelling markedly to a fraction of their size, during which period much less moisture is required.

Vegetative propagation is by division of thick clumps or from cuttings taken from younger stems in autumn, just before the active winter growth season; these methods are essential if one intends preserving particular clones, as progeny from seed can be extremely variable. Cuttings are easily rooted and established in a medium of equal parts coarse river sand and finely milled bark before planting out. Fresh seeds germinate readily when sown in autumn or spring, and can reach flowering stage in 6 months, if well grown.

A word of caution, *Gazania krebsiana* has the potential to become invasive when grown outside of its natural habitat, and *G. linearis* and *G. rigens* have both become naturalised on roadsides and disturbed areas in southern and eastern Australia, in New Zealand and California where they are considered minor environmental weeds.

Gazania krebsiana Less. subsp. **arctotoides** (Less.) Roessler, Mitteilungen der Botanischen Staatssammlung München 3: 405–408 (1959).

Gazania arctotoides Less., Synopsis Generum Compositarum: 48 (1832). Type: South Africa, Cape, Gamka Karoo, collector and precise locality unknown (S, lectotype, designated by Roessler (1959).

Gazania leptophylla DC., Prodr. (DC.) 6: 512. 1838 (early January 1838). Type: South Africa, Northern Cape, Zeekoerivier: *Drège 3716* (G-DC, holotype).

Gazania longifolia Less., Syn. Gen. Compos. 48. 1832 (July to August 1832). Type: not designated (Lessing, 1832; Harvey, 1865; Roessler, 1959).

Gazania pavonia (Andrews) R. Br. var. *zeyheri* Harv. Type: South Africa, Western Cape, Appelskraal: *Zeyher 3015* (S, holotype).

Gazania rogersii S. Moore. J. Bot. 56: 8. 1918. South Africa, Western Cape, Oudtshoorn district: Type: *Rogers 17008* (BM, holotype, Z, isotype).

Description. *Perennial acaulescent herb*, 100–200 mm high. *Rhizome* erect to suberect, 10–30 mm long, slender, branched. *Leaves* basal, tufted, petioled, shape variable, linear to lanceolate, light to dark green or glaucous, simple and entire or pinnatifid, 30–250 mm long, leaflet pairs 3–5, leaflets 3–15 mm long, linear to oblanceolate, upper surface glabrous or white-hairy, lower surface white-hairy; margins revolute. *Scape* 100–200 mm long, reddish-brown, suberect in flower, spreading to decumbent in fruit. *Inflorescence* a radiate, solitary, many-flowered capitulum. *Involucre* campanulate, outer and inner bracts ovate to lanceolate, obtuse or subacute, connate below to form a cup. *Ray florets* in one row, ligulate with flattened tube, infertile; corolla orange, yellow or dark red, lower portion in shades of brown or greenish yellow, with prominent black, iridescent, white or often ocellated basal spot or striation. *Disc florets* bisexual, corolla orange-yellow, tubular, widened above. *Anthers* shortly mucronate-acuminate, bases sagittate. *Cypselas* obovoid-obconical, with rows of swollen cells, sericeous. *Pappus* of many linear scales. Chromosome number: x = 8 (Mehra & Remananandan, 1969); x = 10 (Nordenstam, 1967).

Distribution. Widespread in South Africa in Limpopo, Mpumalanga, Free State, North-West and the Western, Northern and Eastern Cape, and in Botswana.

Habitat. Stony flats and lower hill slopes, often in disturbed sites at roadsides, in full sun.

Flowering time. August to January, with a peak from September to November.

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723. GORTERIA DIFFUSA

Compositae

Graham Duncan and Allan G. Ellis

Summary. The beetle daisy, *Gorteria diffusa* Thunb., is a South African and Namibian spring-flowering annual with a very interesting pollination strategy involving insect-mimicking petal spots, details of which are given here, in addition to notes on its history, habitat and cultivation, accompanied by a watercolour painting of the subsp. *diffusa* and a habitat photograph.

Gorteria is one of about eight genera and 130 species within the tribe Arctotideae, in the subtribe Gorteriinae. Along with other members of this subtribe, it is set apart from genera in subtribe Arctotidinae (which includes *Arctotheca* Vaill., *Arctotis* L. and *Dymondia* Compton, amongst others) in that it possesses latex (Karis *et al.*, 2009). In an investigation into the monophyly of the genera within the Arctotidae and their relationship to one another, using three phylogenetic markers, two from chloroplast DNA (*trn*L-F and *ndh*F) and one from the nuclear genome (ITS), *Gorteria* fell within one of the three monophyletic groups that comprise the Gorteriinae, in the *Gazania-Hirpicium-Gorteria* group; the other groups identified were the *Didelta* group and the *Berkheya-Callumia* group (Funk & Chan, 2008). *Gorteria* is easily distinguished from *Gazania* in having sessile capitula; the receptacles become woody and enclose the fruit after anthesis, and its achenes germinate within the closed receptacle. Unlike most members of the Compositae, in which the achenes act as diaspores, in *Gorteria* the entire lignified receptacle drops off and acts as diaspore (Karis *et al.*, 2009). This is also the case in *Hirpicium alienatum* (Thunb.) Druce and *H. integrifolium* (Thunb.) Less. which are closely related to *Gorteria* (Funk & Chan, 2008; Stångberg, 2009).

Gorteria L. has three species and commemorates the Dutch father and son Johannes and David de Gorter, both botanists and physicists. The first described species was *G. personata* L., an erect, low-growing bushy plant from the Northern and Western Cape that has small spiny flowerheads with short yellow ray florets and dark petal bases (Linnaeus, 1759). The most striking species, *G. diffusa*, was described by the Swede C.P. Thunberg in the late 18th century from an unrecorded locality at the Cape, and his type specimen is preserved in

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his Herbarium at Uppsala University (Thunberg, 1798). The specific name *diffusa* refers to the diffuse or spread-out growth habit of subsp. *diffusa*. A third species, *G. corymbosa* DC. from southern Namibia and the western part of the Northern Cape forms a low spreading bush and has corymbose, yellow flower heads with very hairy involucres; it was described in the early 19th century (De Candolle, 1837).

Gorteria diffusa has three subspecies, subsp. *diffusa*, subsp. *calendulacea* (DC.) Roessler and subsp. *parviligulata* Roessler (Roessler, 1973). In 1826, K.P. Sprengel transferred *G. diffusa* to *Gazania* Gaertn., but in his revision of *Gorteria*, Helmut Roessler (1959) reversed this decision and reduced De Candolle's *Gorteria calendulacea* DC., a sparsely-branched, prostrate herb with reddish orange, cup-shaped flowerheads with black circular centres, to varietal level under *G. diffusa*. More than a decade later, he described the small-petalled *G. diffusa* subsp. *parviligulata* Roessler from southern Namibia, and upgraded the var. *diffusa* and var. *calendulacea* (DC.) Roessler to subspecific level (Roessler, 1973).

Most recently the work of Ellis & Johnson (2009) demonstrates that *Gorteria diffusa* in fact consists of many allopatric variants (referred to as floral morphotypes) which differ substantially in floral and capitulum traits (some of these are illustrated in Fig. 18 on p. 375). Ellis & Johnson (2009) describe 14 discrete morphotypes (named according to the localities at which they occur) and two additional morphotypes were recently discovered in the Richtersveld (Allan Ellis, unpubl.). The morphotypes are allopatrically distributed and never co-occur, except in very narrow contact zones along distribution margins where individuals of intermediate phenotype (hybrids) are also often present. *G. diffusa* has a wide distribution across the winter rainfall zone of southern Africa, occurring from southern Namibia to the Richtersveld, Namaqualand and Western Karoo to the western, southwestern and southern parts of the Western Cape, in South Africa (Roessler, 1959). The subsp. *parviligulata* (probably the Khubus morphotype of Ellis & Johnson, 2009) is only found on the coastal plain of southern Namibia, and subsp. *calendulacea* (the Cal morphotype of Ellis & Johnson, 2009) is endemic to the higher areas of the Kamiesberg in central Namaqualand. The additional 12 described morphotypes of subsp. *diffusa* have equally narrow distributions in Namaqualand and the Little Karoo (Ellis & Johnson, 2009).

Plate 723 *Gorteria diffusa* subsp. *diffusa* Okiep morphotype GEORITA HARRIOTT

The most striking feature of *Gorteria diffusa* capitula are the insect-like ornaments present on some or all of the ray florets. These complex structures, comprising numerous cell types which combine to produce intricate visual, tactile and perhaps olfactory signals, vary dramatically between morphotypes (Johnson & Midgley, 1997; Ellis & Johnson, 2009; Thomas *et al.*, 2009). In some morphotypes they are absent and in others their resemblance to insects is uncanny. Johnson & Midgley (1996) demonstrated that the ray floret spots of the Nieuw morphotype are important for attracting bee-fly pollinators (*Megapalpus capensis* Wiedeman). *Megapalpus* flies are the most abundant visitors to all the *G. diffusa* morphotypes that have been studied, suggesting that the diversity of floral form (and spot structure) does not arise from selection imposed by different pollinator types (Ellis & Johnson, 2009). Instead Ellis & Johnson (2010) showed that spot complexity in some morphotypes is linked to exploitation of mating behaviour of male flies. These spots elicit copulatory attempts from male flies, the first incidence of pollination by sexual deception reported in non-orchid flowers. Thus in *G. diffusa* the petal surface structure and the resulting visual effect depends on which insect behavioural modality (feeding or sex) the plants are exploiting for pollination.

Gorteria diffusa subsp. *diffusa* grows in large colonies on flats and lower rocky hill slopes in gravelly sand or clay, in full sun, and has a long flowering period from late July to early October. This taxon is common in Namaqualand, transforming large tracts into sheets of orange in spring (Fig. 1).

It usually occurs in arid environments with erratic rainfall cycles, and its achenes, enclosed within the receptacle, are long-lived and capable of surviving years of drought. Judging from the erratic germination results obtained in cultivation, viable seeds appear to have an in-built mechanism preventing them all germinating during the same season, irrespective of whether favourable conditions exist for them to do so, thus ensuring a continuous reservoir of viable seeds in the soil as an insurance against detrimental climatic conditions, such as periods of drought that may occur during the active growing season.

CULTIVATION. All three *Gorteria* species are winter-growing annuals and have more or less the same cultivation requirements. Despite the striking beauty of *G. diffusa* subsp. *diffusa,* it is seldom cultivated as

Fig. 1. *Gorteria diffusa* subsp. *diffusa* in habitat near Bitterfontein, southern Namaqualand. Photograph: Graham Duncan.

the plants are highly sensitive to soil moisture and air humidity, the seedlings and mature plants rapidly succumbing to fungal infection. The plants require full sun and a dry atmosphere, and in suitable climates are suited to mass planting in rock garden pockets and to troughs or window boxes, in gritty media. Mature plants and seedlings should be allowed to dry off almost to the point of wilting before the next drench is applied.

The receptacles containing the achenes are 'sown' just below soil level in autumn in a well drained sandy-gritty medium, in a protected position, in bright light. Germination is erratic in that only one or two achenes may germinate, the others remaining dormant for one or more seasons. In ideal conditions, seedlings reach flowering stage in three to four months.

In temperate climates it should be noted that *Gorteria personata* has become naturalised along roadsides in Western Australia, where it is considered a noxious weed (Hussey *et al.*, 1997) and the same potential may exist with *G. diffusa*.

Gorteria diffusa Thunb. subsp. **diffusa**, Skrivter Naturhistorie Selskabet 4(2): 2 (1798). Type: South Africa, Cape, precise locality unknown, holotype in Herb. Thunberg (UPS).

Gazania diffusa (Thunb.) Spreng., Systema vegetabilium 3: 606 (1826). Type: as above.

Ictinus piloselloides Cass., Bull. Soc. Philom.: 142 (1818). Type: South Africa, Cape, precise locality unknown, *Sonnerat s.n.* (P, holotype).

Gorteria ictinus Cass., Dict. Sc. Nat. (ed 2), 33: 455 (1824). Type: as above.

Gorteria affinis DC., Prodromus systematis naturalis 6: 501 (1837). Type: South Africa, Northern Cape, Groenrivier, *Drège 494* (G-DC.) (syntype); Kamiesberg, *Ecklon & Zeyher* 73 (G-DC.) (syntype).

DESCRIPTION. *Winter-growing annual,* 5–30 cm high. *Plant* sprawling, branching from base, with slender taproot and numerous fibrous lateral roots. *Stems* cylindrical, diffuse, hairy, light green. *Leaves* linear, lanceolate or oblanceolate, alternate, 20–50 × 5–8 mm, light green, upper surface hairy, lower surface woolly, entire, toothed or pinnatifid, mostly sessile, lower leaves tapering into a short petiole, margins revolute. *Capitula* radiate, solitary, sessile, terminal, 20–35 mm in diam. *Involucre* ovoid; bracts acuminate, hairy to tips, united towards base into a more or less urceolate cup, pungent, enclosing fruit after anthesis. *Receptacle* basin-shaped. *Ray florets* ligulate, 12–20 × 4–6 mm, sterile, narrowed at base into long claw, orange above, purplish dorsal stripe below, with dark basal, glossy spot on 1, (usually two or 3) or rarely 4 florets, each with a small white reflective dot. *Disc florets* orange, outer florets mostly female-sterile, inner florets male, corolla with five linear or lanceolate lobes. *Anthers* shortly sagittate at base, apical appendage ovate. *Style* linear, subglobose at base, branches linear-lanceolate. *Cypselas* obovoid, apically sericeous. *Pappus* of minute scales, hidden between cypsela hairs; achenes germinating within the closed receptacle. *Chromosome number*: unknown.

DISTRIBUTION. Southern Namibia and in South Africa from the northern Richtersveld, Namaqualand and western Karoo to the western, southwestern and southern Western Cape.

HABITAT. Flats and lower rocky hill slopes in gravelly sand or clay, in full sun.

FLOWERING TIME. July to October, with a peak in August and September.

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THE CONTRIBUTION OF EPIDERMAL STRUCTURE TO FLOWER COLOUR IN THE SOUTH AFRICAN FLORA

Heather M. Whitney, Beverley J. Glover, Rachel Walker
and Allan G. Ellis

Summary. This paper aims to introduce very briefly the effect of the petal epidermal surface on floral colour and pollinator interactions. Details of the structure of *Spiloxene capensis*, *Geissorhiza radians, Moraea villosa*, *Moraea loubseri* and the different morphotypes of *Gorteria diffusa* are illustrated and their significance explained.

The flora of South Africa is known for its incredible species richness and its corresponding wide range of interactions with animals. Recent work is beginning to suggest that the South African flora might also be diverse in an additional factor that is rarely considered – its production of floral iridescence. This diversity of floral iridescence was first reported in any detail in Marloth's *The Flora of South Africa* in 1915. As well as presenting an utterly stunning example of a botanical study, this book provides some remarkably accurate information about the contribution of structural elements to the range of optical effects shown by endemic South African flowers. That modern research is only just beginning to unpick the biological and physical basis of the optical effects produced by floral surface structure makes the discoveries described in Marloth's *The Flora of South Africa* all the more striking.

Importance of structural contributions to floral colour in the South African flora

Why is the structural contribution to floral colour thought to be of importance in the South African flora? One hypothesis is the diversity of plant-pollinator interactions found in this region. For example, most of the species discussed in this volume produce spots on their petals with a high degree of contrast – due to differences in both pigment and structure – with the rest of the petal (Thomas *et al.*, 2009). It is on these spots that floral iridescence is frequently located, and the striking similarity between these spots and pollinators, such as monkey beetles *Anisonyx ditus* and *Peritrichia rufotibialis* or *Megapalpus* flies, many of which produce iridescence of their own (Seago *et al.*, 2009), has led to the suggestion that the spots have evolved to

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enhance visitation by these pollinators (Johnson & Midgley, 1997; Steiner, 1998).

Floral colour

To begin to understand the diversity of mechanisms by which the South African flora produces its vivid colours, we must first establish what floral colour is and the range of mechanisms by which it is currently known to be produced. This will be a very brief overview – partly for brevity, particularly as several recently published books and articles describe these mechanisms in great detail (Glover & Whitney, 2010), but also because this is an ongoing field of study. The discovery that diffraction gratings can be produced by the floral epidermis and can produce iridescence in the ultraviolet that can be perceived by insect pollinators, was only described in 2009 (Whitney *et al.*, 2009).

Colour is a property of both the coloured object and the visual system by which it is perceived. Light can be transmitted through, absorbed by or reflected back from any object. An object which strongly reflects specific wavelengths can be said to have a colour. What that colour is depends on the visual system observing the object. If it has photoreceptors that are strongly activated by the specific (for example blue light) wavelengths, then the object will be perceived as blue. If it has no photoreceptors that respond to blue light, the object will appear black, as no other wavelengths are received by the visual system. The photoreceptors present differ across the visual systems of different animals; for example the human visual system contains photoreceptors for blue, green and red, while ultraviolet, blue and green occur in the visual system of the bee.

Plants, like any other object, can achieve colour in two main ways. The most widespread, and the one about which most is known, is chemical- or pigment-based colour. Pigments are compounds which absorb subsets of the visible spectrum, transmitting and reflecting back only what they do not absorb and causing the tissue to be perceived as the reflected colours. For example, the perception of plants as ‘green’ to the human eye is due to chlorophyll, which absorbs light in both the red and the blue parts of the spectrum, reflecting only green light. Pigments that produce floral colour include the flavonoids (an incredibly diverse group that produces colours ranging from whites and creams to dark purples) and the carotenoids (which produce mainly yellows and oranges) (Kay *et al.*, 1981).

The second way to produce colour, shown in both animals and plants, is known as structural colour. A structural colour occurs when (as the name suggests) structures on the surface of an object, usually at or around the wavelength of light in size, cause different wavelengths of light to be selectively reflected from a substance, with the remaining wavelengths transmitted or absorbed. Examples of everyday structural colours can be seen in the shifting shades on the back of a compact disk (caused by a diffraction grating), or on the rainbow shimmer seen on an oil slick on a puddle (thin-film interference).

Chemical and structural colours have several different properties. They differ first in the intensity of colour that they produce. Pigments generally both absorb and reflect a broad range of wavelengths. This means that the colours they produce can appear dull or muted, as they consist of a mixture of different colours of light, particularly when compared with structural colours which can appear very intense, as reflective structures can be very precise in the bandwidths that they reflect. The different properties of structural or pigment colour will have different advantages to flowers in different habitats or when interacting with different pollinators. The various selection pressures on the optical properties of flowers have been important in generating and maintaining their diversity.

Contributions of surface structure to floral colour

Structures associated with the petal epidermis can affect the hue (colour) perceived in a variety of ways. The epidermal surface can indirectly influence the optical properties of the flower without altering its hue (in much the same way that a piece of cloth dyed with the same pigment will look utterly different if the fabric is velvet, satin or cotton) or through directly impacting on floral colour.

In 1994 researchers at the John Innes Centre in Norwich isolated a mutated line of *Antirrhinum majus*. This line was identified due to the colour of the flowers it produced, which were a washed-out pink rather than the vibrant magenta found in the wild-type flowers. This line was found to have a mutation in a gene that had no effect on pigment biosynthesis, but instead altered the structure of the petal epidermis.

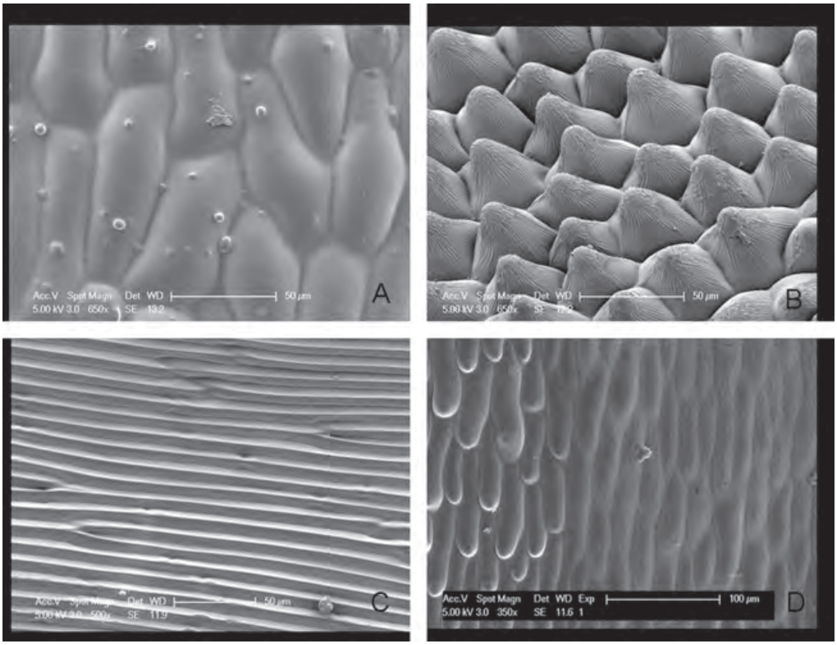

Fig. 1. Scanning electron microscope images of some of the variation found in petal epidermal cell form. *Nymphaea alba* (A) lacks conical cells completely while (B) *Helianthus annuus* has striations on the conical cells, (C) *Eschscholzia californica* has elongated prism shaped cells and (D) *Hibiscus trionum*, has a mixed petal epidermal morphology of both conical cells non-striated cells and flat striated cells.

A. majus, like about 80% of other species examined, produces cone shaped cells on its petal epidermis. The widespread occurrence of these structures on the petal epidermis, and their absence from other plant surfaces, had been noted by many earlier researchers including Marloth in *The Flora of South Africa* and a corresponding range of hypotheses as to their function had been suggested. The mutant line of *A. majus* lacking these conical cells provided an ideal opportunity to test these ideas (Glover & Martin, 1998). That the flat-celled flowers were a different colour to the conical celled flowers indicated that the structure of the petal surface could have an important role in the final colour of a flower. In this case it was found that the conical cell shape enhanced the pigment colour by focusing the light that reached the petal into the region of the epidermis where the pigment is contained (Noda *et al.*, 1994; Gorton & Vogelmann, 1996), a mechanism suggested by Marloth (1915). There is a huge degree of variation in the petal epidermal cell form, with variation both in the size and shape of the overall cell (Figure 1). The differences in size and shape of these petal epidermal conical cells could potentially result in different interactions between light and floral pigments, with different cell shapes interacting with pigments in different ways, increasing the diversity of the colours that flowers can potentially produce.

The floral surface may also produce a range of other optical effects, including glossiness and iridescence.

Iridescence in flowers

There may be an advantage to flowers producing structural rather than pigment based colours. When not modified by the petal surface, pigment based colours are usually diffuse, and look the same from all angles. In order for them to produce any pattern or variety of colour, different pigments must be localized to different areas of a flower. On the other hand, structural colours have the potential to generate shifting patterns of colour as the viewer moves, rather than across different regions of the tissue. Reflective structures can reflect one particular peak wavelength of light at one angle, and another peak wavelength at a second angle. Thus, as a pollinator moves its position relative to the flower it will see the object change from the first colour to the second colour. The phenomenon of appearing different colours when viewed from different angles is called iridescence, and it is a unique attribute of structural colour. Iridescence can cover a few or many different colours, and can be in regions of the spectrum visible to a variety of animals, including in the ultraviolet (UV).

The suggestion that petal epidermal striations could be involved in floral colour production had been postulated by Marloth (1915), but which colours could be produced and how these structures produced colour was not demonstrated. Recently, diffraction gratings capable of producing iridescence were noted in plants, with the first report of their presence on the petals of species including *Tulipa* sp. (Fig. 2), and *Hibiscus trionum* (Fig. 1D) (Whitney *et al.*, 2009). In these species the petal epidermal cells are elongated and flat and the overlying cuticle produces a series of long, ordered ridges with a periodicity that acts as a diffraction grating and splits the light reflecting from the surface into component wavelengths.

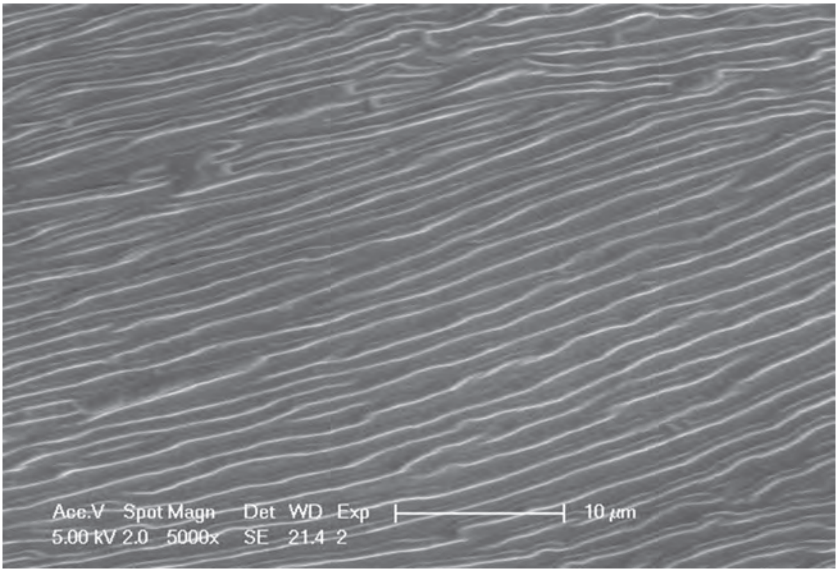

Fig. 2. Scanning electron microscope image of the ordered epidermal striations found on the tulip variety 'Queen of the Night'.

The iridescence produced is often predominantly in the UV wavelengths, which, although invisible to the human eye, are easily visible to many animal pollinators including bees and birds. These petal epidermal striations have been found in many species of flowering plants, so this mechanism of producing floral colour is thought to be extremely widespread, and may be important in plant-pollinator interactions.

Flowers can also produce structural colour by other mechanisms, and are the site of the one example of a three-dimensional photonic structure that has been found in plants. The elongated hairs that cover the attractive bracts surrounding edelweiss flowers (*Leontopodium nivale* subsp. *alpinum*) have an internal structure that acts as a photonic crystal (Vigneron *et al.*, 2005). The structure of the hairs means that they absorb the majority of the UV light, effectively acting as an efficient sun-block, which is thought to be a protective advantage against UV damage in this mountain flower.

Marloth's The Flora of South Africa

Some of the earliest insights into the complexity of mechanisms by which flowers produce visual signals, were undoubtedly contributed by Dr Rudolf Marloth, a distinguished botanist working in the Cape in the late 19th and early 20th centuries. He was by profession an analytical chemist, and clearly his knowledge of chemistry and physics strongly influenced his detailed observations of floral structure and his interpretation of its functional mechanisms. His contributions to our knowledge of the Cape flora were vast, but one of his pet interests appears to have been the production of unusual floral signals and particularly the colour green, as exemplified by this statement, 'excepting some species of heath, e.g. *Erica sessiliflora* and *E. tenax*, in which the corolla does contain chlorophyll-granules in the cells below the outer epidermis, so far no green pigment has been found by me in any of these cases'. In his impressive work *The Flora of South Africa* (published in six volumes between 1913 and 1932) Marloth makes reference to many observations of alternative, unusual mechanisms for the production of floral colour, some of which are described in more detail below, and some of which are explored elsewhere in this issue.

Fig. 3. Iridescent spots on the flowers of *Moraea villosa*. (see ~~below~~).

Marloth's investigations into epidermal cell shape

Marloth was acutely aware of the influence of the shape of the petal epidermal cells on the production and quality of colour. For example, he attributed the golden glitter on the bright red petals of *Nerine sarniensis* to a structural optical mechanism. The epidermal cells, which contain red pigments, are pear shaped with the narrow end of the cell abutting against the internal unpigmented cells which are surrounded by air spaces. The majority of light entering the convex upper surface of the epidermis is prevented from penetrating further into the petal by the air spaces because 'a ray of light cannot pass from water into air unless the incident angle be larger than 45°'. Thus the structure of the epidermal cells and the inner petal tissues result in light being bounced around within individual epidermal cells and ultimately being reflected as pure red wavelengths through the centre of the convex outer cell surface, resulting in the glittering effect which so fascinated Marloth. He proposed that a similar mechanism produces the brilliant blues of *Disa graminifolia* and in *Disa uniflora* he found that the epidermal cells also act as light traps, but no light is able to pass through them because of a layer of yellow chromatophores at their base.

The velvety sheen which characterizes the unusually coloured portion of the perianths of many Cape species (e.g. *Spiloxene capensis*, the peacock Moraeas and *Gladiolus orchidiflorus*) was suggested by Marloth to result from the presence of elongated narrow papillae on the epidermal cells of these species. He proposed that light is continuously reflected between and within these tall cell structures resulting in light reflected from these surfaces having the deep and saturated colours of a velvet surface.

Colour mixing: fat droplets and crystalline structures

Some of the most distinct iridescence occurs in *Spiloxene capensis*. The vivid iridescence shown by this flower was highlighted in the *The Flora of South Africa* by Marloth's use of a particular type of paint used solely for this picture – both the iridescent green centre of this flower and the metallic green monkey-beetle shown pollinating the flower are hand-painted with a metallic green paint. Marloth also noticed that the brilliant metallic green centres of the flowers of some forms of *S. capensis* do not contain green pigments. Instead they contain the

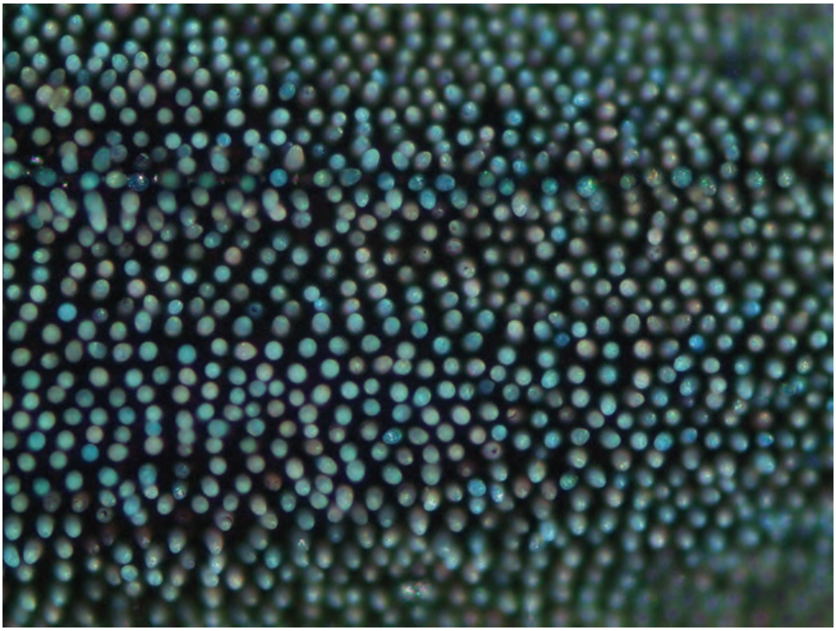

Fig. 4. The metallic green colouration shown by the iridescent spot in some forms of *Spiloxene capensis*. Photograph ~~by~~ Allan Ellis.

same dark purple substance as the cells of the maroon portions of the petals, but differ dramatically from these structurally. Each cell ends in a tall conical papilla filled with 'colourless, angular, highly reflective granules of a fatty substance' (see Figs 4, 5, & 6). Marloth proposed that the green colour results from optical interference in this colourless granular mass. The occurrence of these structures is discussed in more detail below.

In *Gladiolus orchidiflorus* Andrews, Marloth found the unusual green colour of the three lower perianth segments to result, not from pigments, but from optical interference resulting from intermingled yellow chromatophores and colourless calcium oxalate crystals in the epidermal cells.

In the daisy, *Ursinia anethifolia* N.E. Br., the cells of the involucral bracts underlying the translucent bases of the ray florets contain colourless refractive granules in a pale yellow protoplasm which generate the dark green ring in the capitulum.

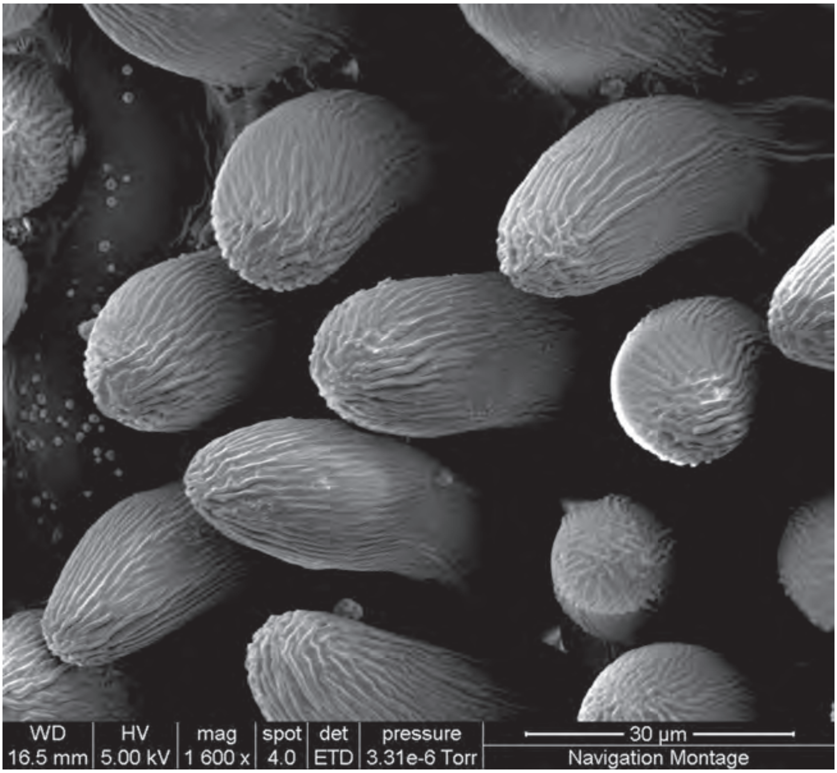

Fig. 5. Scanning electron microscope image of the striated conical cells of *Spiloxene capensis* tepals. ~~Image by~~ Heather Whitney.

Colour mixing: pigment combinations

In *Moraea tulbaghensis* (see plate 719), one of the peacock moraeas, which are characterised by velvety green-black central spots on their tepals, Marloth found that the green colour results from the combined effect of blue sap and yellow chromatophores in the epidermal papillae. He further suggested that the velvet-like deep and saturated colours result from reflectance of light between adjoining long narrow papillate epidermal cells. In *Gazania rigens* (L.) Gaertn., the black marks at the centres of the ray florets result from a combination of blue pigmented cell sap and orange granules contained therein.

Surface striations

Marloth was perhaps the first researcher to suggest that surface striations on the petal epidermis could produce structural colour.

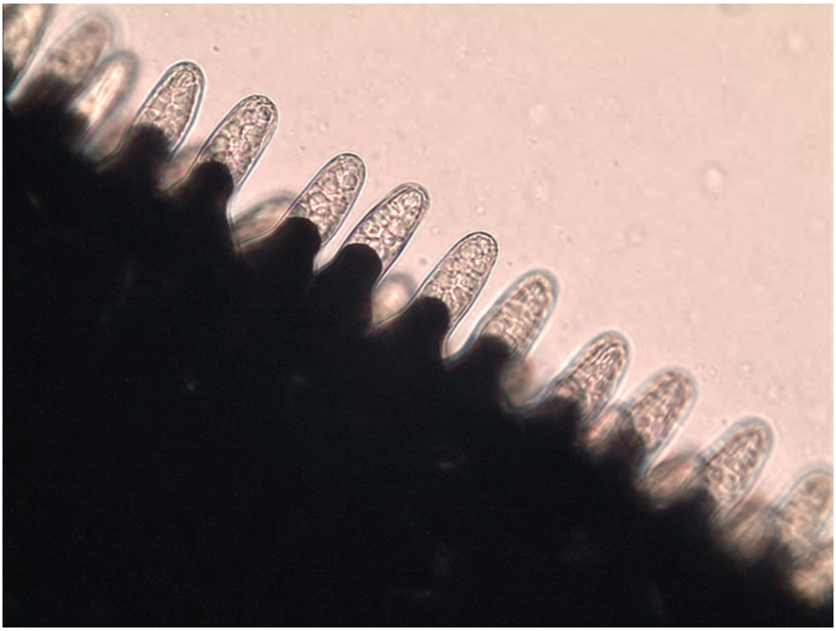

Fig. 6. Light microscope photograph of cells of iridescent region in *Spiloxene capensis* with clear, granules overlying the dark purple pigment found elsewhere in this flower. Photograph ~~by~~ Allan Ellis.

Ixia viridiflora produces flowers with an unusual greenish blue hue; he suggested that the greenish hue did not result from pigments, but from a combination of optical reflective effects caused by the finely striated outer cell walls and highly refractive granules in the epidermal cells. However, our recent work (Whitney *et al.*, unpubl.) has found that the petal epidermal striations on *I. viridiflora* are not sufficiently ordered to produce structural colour. Research into the contribution of structure to the unusual colour produced by *I. viridiflora* is still ongoing.

SPILOXENE

Spiloxene capensis is the only member of the genus possessing iridescence, seen as a deep blue or emerald green triangular zone.

Marloth suggested that the iridescence zone in the centre of the flower is caused by a novel mechanism. He noticed that the brilliant metallic green region does not contain any green or blue pigment. Instead it contains the same dark purple pigment as the cells of the dark, non-iridescent portions of the tepals, but differ

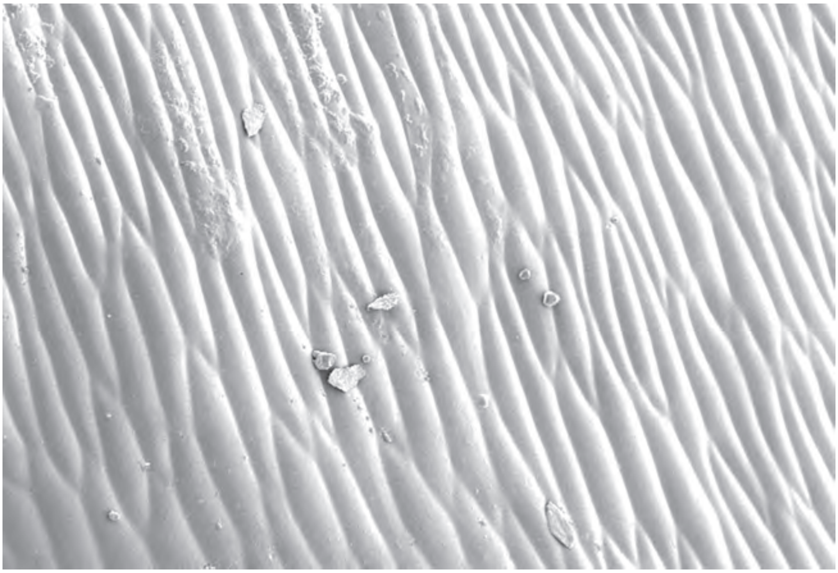

Fig. 7. Scanning electron microscope image of the epidermal cells of *Geissorhiza radians*.

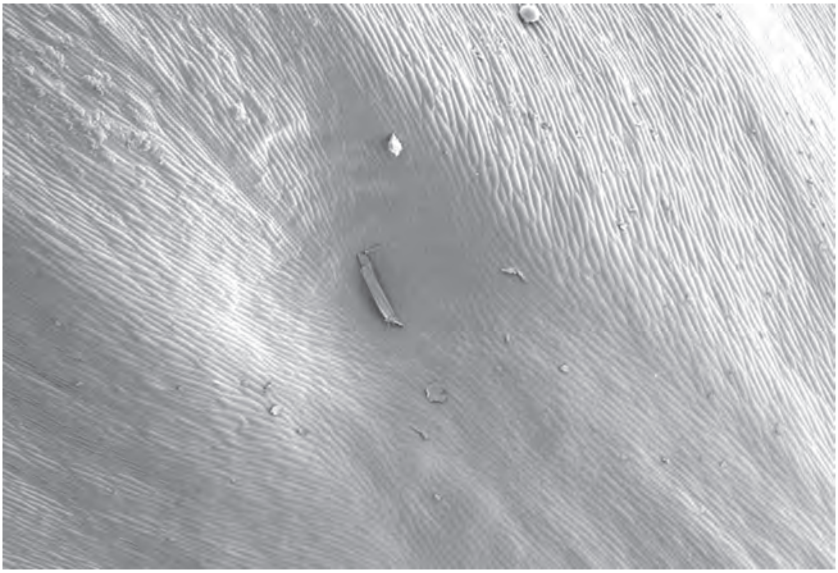

Fig. 8. Scanning electron microscope image of the pit region of *Geissorhiza radians*.

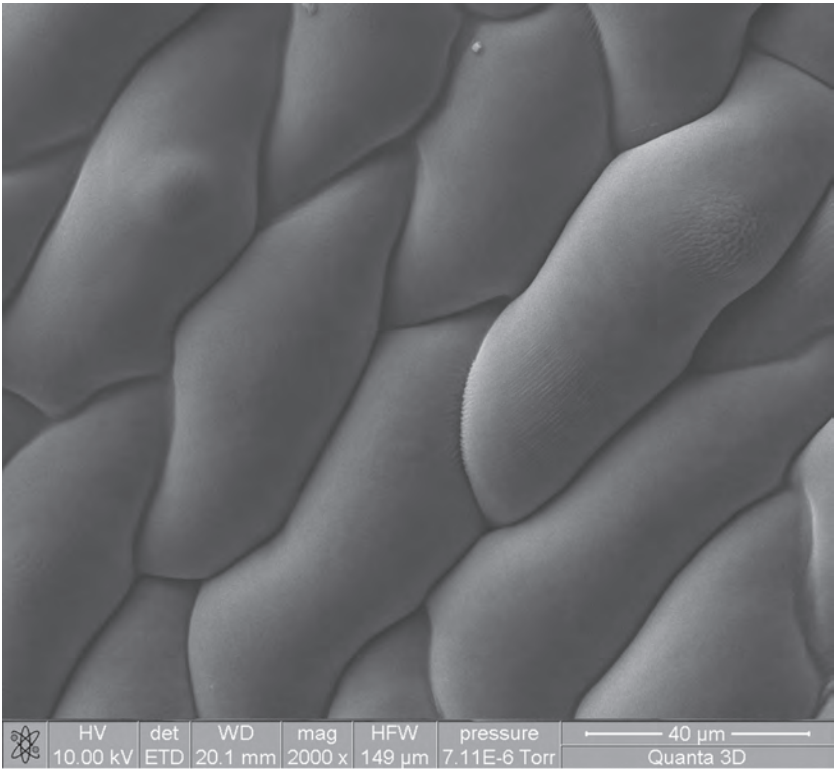

Fig. 9. Scanning electron microscope image of the lenticular cells that cover the majority of the petal surface in *Moraea villosa*. Scale bar is included in image. Photograph: Heather Whitney.

dramatically from these structurally. Each cell ends in a tall conical papilla filled with 'colourless, angular, highly reflective granules of a fatty substance'. Marloth proposed that the green colour results from optical interference in this colourless granular mass. Recent investigation into the iridescence present on *S. capensis* has found that there are structural differences in the epidermis in this region of the tepal. Striated, elongate conical cells do occur in this region (see Fig. 6), and as Marloth discovered, we also find that colourless granules occur in the tips of these conical cells, and that below these granules the dark purple pigment found elsewhere in the tepal can be seen. What these colourless globules contain and how, or indeed, if, they produce the striking iridescence found in the centre of many *S. capensis* flowers is still the subject of ongoing research.

Geissorhiza radians

In *Geissorhiza radians* (see above) the deep brown pits were initially expected to have iridescence. These regions have a high degree of gloss, to the extent that one of the common names of this flower is ‘Red Sequin’. Analysis of the tepal surface shows that the epidermal surface of the pit is composed of flat cells, as is the rest of the tepal epidermal surface (Fig. 7).

However, the dip in the surface where the pit is located is clearly visible under the scanning electron microscope (Fig. 8). This suggests that rather than the petal epidermis producing any form of iridescence, these highly flat cells are responsible for predominantly specular reflection, which causes the high degree of gloss found on this flower.

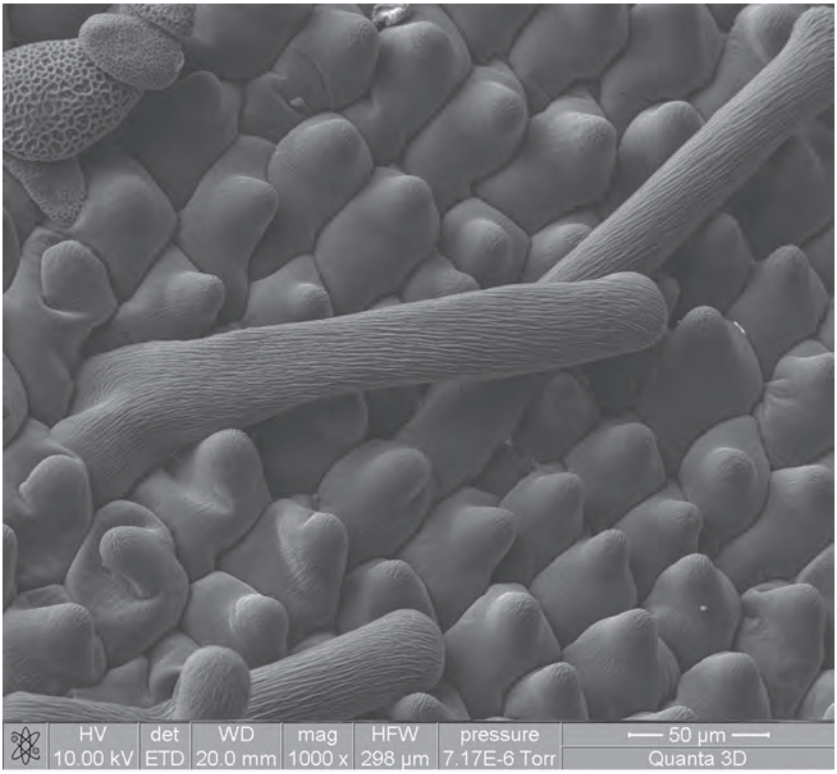

Fig. 10. Scanning electron microscope image of the two types of conical cells found towards the base of the tepal in *Moraea villosa*. Scale bar is included in image. Photograph: Heather Whitney.

MORAEA VILLOSA

The epidermal structure of the upper surface of *Moraea villosa* (Fig. 3, plate 720) varies over the tepal, with differences in structure usually occurring where there are differences in pigmentation. Scanning electron microscope images show that the outer region of the tepal consists of lenticular cells, which protrude out from the tepal's surface much less than the conical cells found in *Moraea loubseri*.

The inner region of the tepal is pubescent, and like *Moraea loubseri* this region is composed of elongated striated structures, that may be related to the extended conical cells found in the regions between the lenticular (Fig. 9) and pubescent regions (Fig. 10). These could be the elongated narrow papillae to which Marloth attributed the velvety sheen which characterizes this peacock Moraea. He also proposed that neighbouring papillae produce different coloured pigments,

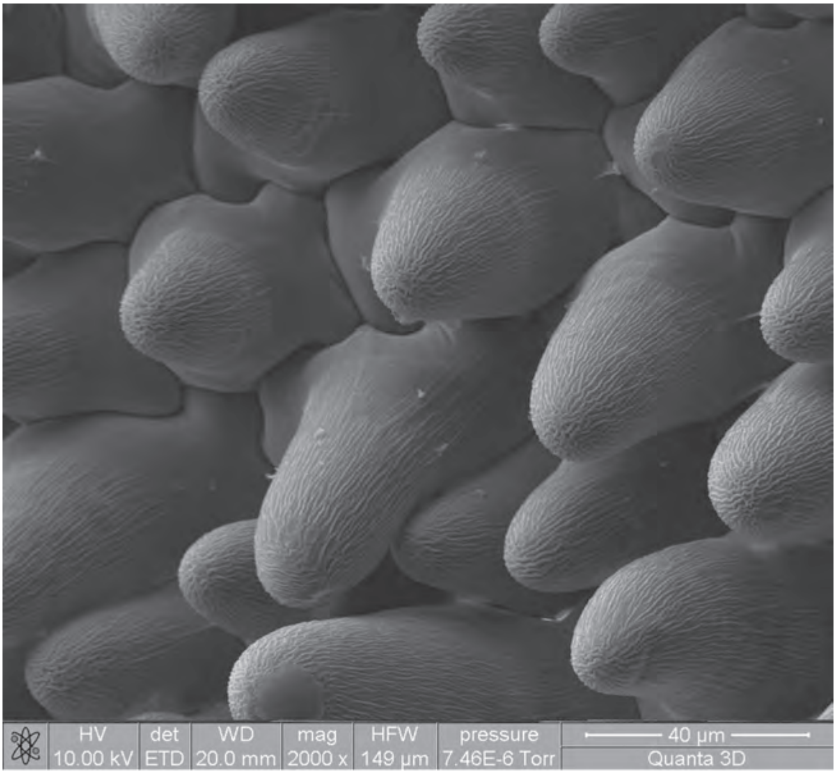

Fig. 11. Scanning electron microscope image of the conical cells that cover the majority of the tepal surface of *Moraea loubseri*. Scale bar is included in image. Photograph: Heather Whitney.

which thus produce the ‘two-tone’ effect seen in the iridescent spot on these flowers (Marloth, 1915).

Moraea loubseri

The epidermal surface structure of the *Moraea loubseri* upper tepal consists of extended conical papillate cells over the majority of the surface (see above). These conical cells are striated (Fig. 11). The upper surface of the inner, bearded tepal region appears to consist of extended ‘hair’ structures that are striated in a similar fashion to the conical cells (Fig. 12), however how these structures are produced is as yet unknown. It is known that structured hairs on the surface of flowers such as the edelweiss (*Leontopodium nivale* subsp. *alpinum*) have photonic effects (Vigneron *et al.*, 2005), and selectively absorb light wavelengths in the ultraviolet region of the spectrum.

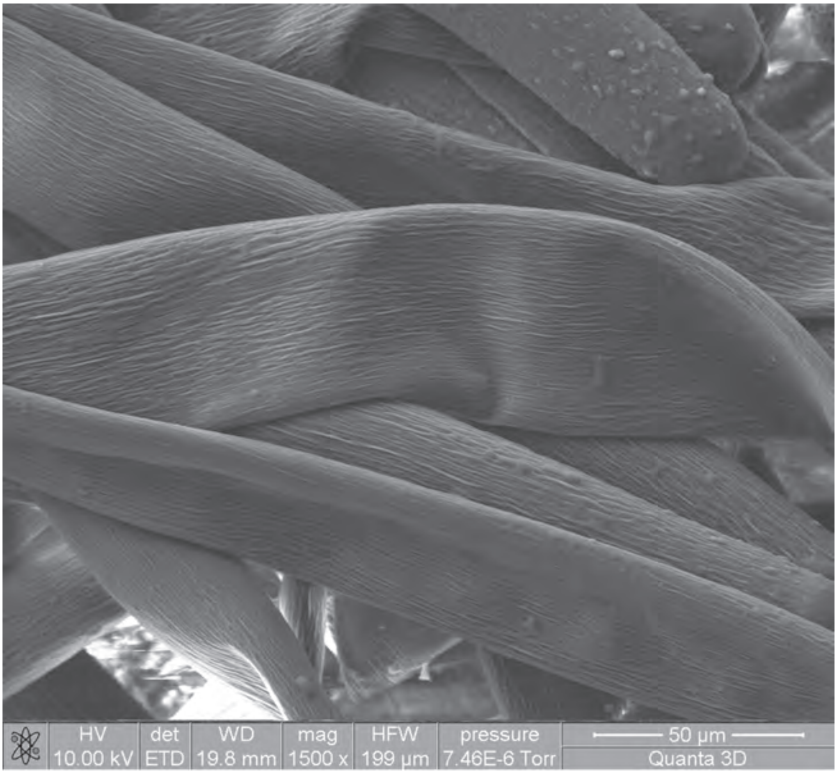

Fig. 12. Scanning electron microscope image of the hairs that cover the bearded region of the tepal of *Moraea loubseri*. Photograph: Heather Whitney.

Fig. 13. Scanning electron microscope image of overall petal spot morphology on a ray floret of *Gorteria diffusa*, Spring morphotype. Photograph: Craig Perl.

BEETLE DAISY

GORTERIA DIFFUSA

Petal spots have evolved across a phylogenetically broad range of angiosperm families; many species with petal spots belong to the Iridaceae, Liliaceae and Asteraceae families. The petal spot in *Gorteria diffusa* Thunb. is a significant floral feature; pollinator behaviour studies suggest that it may function to attract the bee-fly *Megapalpus capensis* Wiedeman (Johnson & Midgley, 1997). Petal spots are composed of a contrasting pigment in a group of cells of the petal epidermis and in

Fig. 14. *Gorteria diffusa*. Scanning electron microscope image of the petal spot cell types: large papillae cells that contain a concentrated deposition of anthocyanin pigment, highlight patches of cells with a smooth surface that do not contain anthocyanin pigment and interior cells, which are striated and contain both chlorophyll and anthocyanin pigments. Photograph: Craig Perl.

a small number of species, the spot is also composed of different cell morphologies, including the specialised conical-papillate cells that increase petal attractiveness (see Fig. 13), (Noda *et al.*, 1994).

Gorteria diffusa (see Fig. 15 and Plate 723) is one of these species that has petal spots composed of both pigment and specialised cell shapes, which may give this spot an insect-like appearance, increasing attractiveness to pollinators. The *Gorteria* petal spot consists of up to three cell types: large papillae cells containing a concentrated

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Fig. 15. **Gorteria diffusa** subspecies and morphotypes: left to right, top row: capitulum of Khubus morphotype, × 1; capitulum of Soeb morphotype, × 1. Second row: ray floret of Cal morphotype (*G. diffusa* subsp. *calendulacea*), × 3; capitulum of Cal morphotype (*G. diffusa* subsp. *calendulacea*), × 1; ray floret of Okiep morphotype, × 3; capitulum of Okiep morphotype, × 1. Third row: capitulum of Spring morphotype which has failed to develop a spot, × 1; capitulum of Spring morphotype with single spot, × 1. Fourth row: capitulum of Spring morphotype with two spotted ray florets, × 1; ray floret of Spring morphotype with incompletely developed spot showing specialized cells, × 3; capitulum of Naries morphotype, × 1. Painted by Georita Harriott from plants cultivated at the University Botanic Garden, Cambridge.

Fig. 15. *Gorteria diffusa* (caption opposite) GEORITA HARRIOTT

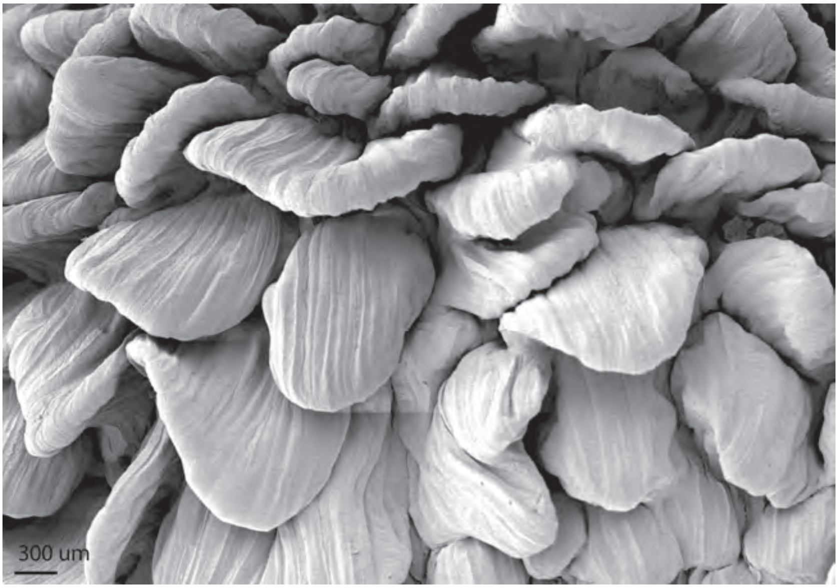

Fig. 16. *Gorteria diffusa*. Scanning electron microscope image of the large papillae cells that contain a concentrated deposition of anthocyanin pigment. Photograph: Craig Perl.

deposition of anthocyanin pigment (see Fig 14), highlight patches composed of cells with smooth surfaces that contain no anthocyanin pigment (see Fig. 17), and striated interior cells, which contain both chlorophyll and anthocyanin pigments (see Fig. 18) (Thomas *et al.*, 2009).

Gorteria diffusa is also an interesting species in which to study petal spot evolution, because within a restricted distribution from the Western Cape to Namibia, this species exists as a complex of several geographically identifiable populations, termed 'morphotypes' (see *Gorteria diffusa* by Duncan and Ellis, Plate 723). These morphotypes have distinct petal spots, which vary in their morphology, including the amount of pigment, type of specialised cell shapes and the number and position of petal spots on the capitulum.

To discover how petal spots develop, genes that encode the regulators of petal spot morphology (cell shape and anthocyanin biosynthesis) are being characterised. To determine how this specialised floral feature has evolved in *G. diffusa*, the genes that encode the regulators of petal spot morphology are being compared to the spot phenotype of the different morphotypes.

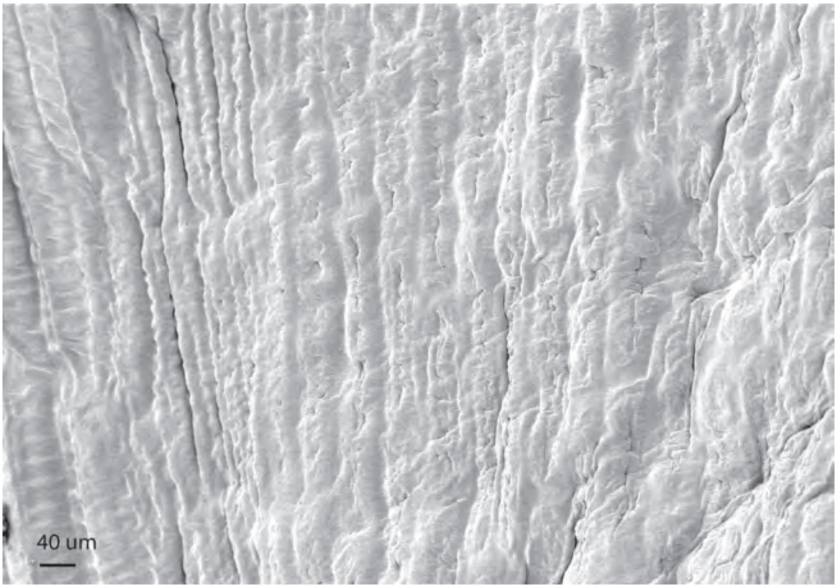

Fig. 17. *Gorteria diffusa*. Scanning electron microscope image of a highlight patch of cells, which have a smooth surface and do not contain anthocyanin pigment. Photograph: Craig Perl.

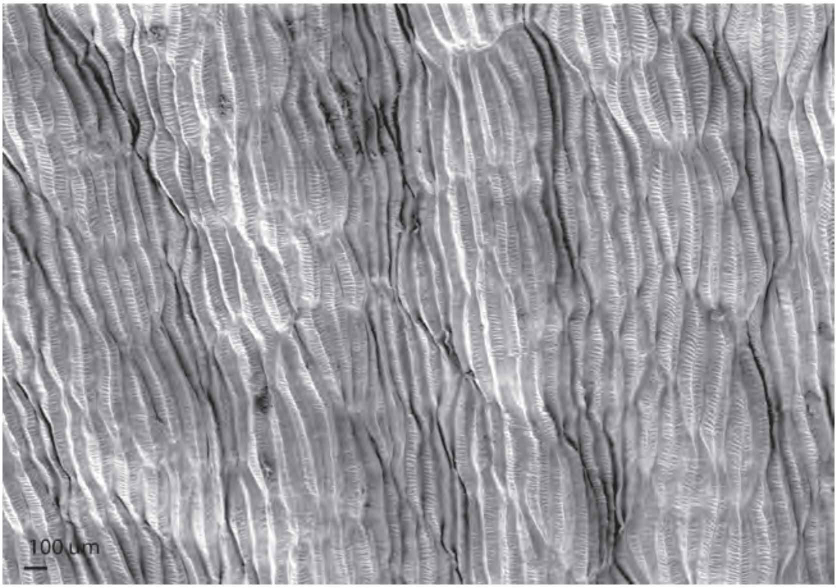

Fig. 18. *Gorteria diffusa*. Scanning electron microscope image of the interior cells, which are striated and contain both chlorophyll and anthocyanin pigments. Photograph: Craig Perl.

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CONTRIBUTORS

Graham Duncan is the specialist horticulturist for southern African bulbous plants at the National Botanical Garden, Kirstenbosch, with a particular interest in the cultivation and propagation of southern African bulbous plants and the taxonomy of the genus *Lachenalia*. Address: National Botanical Institute, Private Bag X7, Claremont 7735, South Africa. E-mail: Duncan@sanbi.org.

Allan G. Ellis has a particular interest in floral evolution and pollinator/flower interactions in the Cape flora. He has been studying floral diversity within *Gorteria* in collaboration with the Plant Sciences department at Cambridge. Address: Botany and Zoology Department, Stellenbosch University, Private Bag X1, Matieland 7602. E-mail: agellis@sun.ac.za.

Beverley J. Glover is Reader in the Evolution and Development laboratory in the Department of Plant Sciences at the University of Cambridge. She studies the interaction of floral surfaces with pollinators, and has worked with *Antirrhinum majus* and *Ophrys* spp. E-mail: bjg26@cam.ac.uk.

Peter Goldblatt is a specialist on the Flora of South Africa, who has published many monographs of different genera, particularly of the Iridaceae, as well as the recent *Cape Plants. A Conspectus of the Cape flora* (2000), with John Manning. He is B.A. Krukoff Curator of African Botany, Missouri Botanical Garden, P. O. Box 299, St. Louis, Missouri 63166, USA. E-mail: peter.goldblatt@mobot.org.

Georita Harriott is a freelance botanical illustrator. She has a BA honours degree in scientific illustrations and art history. She has contributed to many botanical works including the recent Curtis's Botanical Monograph on the genus *Lavandula* and the special part on the University Botanic Garden, Cambridge. Address: 1 Gravel Hill Cottages, 181a Huntingdon Road, Cambridge, CB3 0DJ. E-mail: georitaharriott@finebotanicalprints.co.uk.

John C. Manning is a specialist on the Cape Flora, particularly *Gladiolus*, and is the author of many publications notably the recent *Cape Plants. A Conspectus of the Cape flora* (2000), with Peter Goldblatt. Address: Compton Herbarium, South African National Biodiversity Institute, Private Bag X7, 7735 Claremont, Cape Town, and the Research Centre for Plant Growth and Development, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, Private Bag X01, Scottsville 3209, South Africa. E-mail: j.manning@sanbi.org.za.

Rachel Saunders has a PhD in microbiology, but now owns and runs (with her husband Rod) a small business specialising in the sale of seeds native to Southern Africa. They travel extensively in Africa, walking in the mountains and photographing plants. They grow many SW Cape bulbous and cormous plants, particularly rare and endangered species, with the idea of getting them into horticulture to conserve them. E-mail: silverhill@yebo.co.za.

Lucy Smith is an Australian botanical artist and illustrator who is based in the Palm Room of the herbarium at Kew. She has received various awards for her scientific illustrations and paintings, including the Linnean Society's Jill

Smythies' medal, two gold medals from the Royal Horticultural Society, and second prize and highly commended Flockton awards in Sydney. In 2001 she took part in a BBC documentary filmed on the replica of HM bark (or barque) *Endeavour*, taking on the role of Sydney Parkinson as natural history illustrator to the expedition. E-mail: l.smith@kew.org.

Rachel Walker is a PhD student in the department of Plant Sciences in the University of Cambridge, studying the evolution of the petal spots in *Gorteria*. E-mail: Rachel.Walker@plantsci.cam.ac.uk.

Heather M. Whitney did her PhD at the University of Cambridge, and is now ERC Research Fellow at the School of Biological Sciences of the University of Bristol. Address: Woodland Road, Bristol, BS8 1UG. E-mail: Heather.Whitney@bristol.ac.uk.

CURTIS'S BOTANICAL MAGAZINE

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or
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