SPARAXIS EXPANDED

A review of a Cape genus and its biology.

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The red sparaxis, *Sparaxis pillansii*, a narrow endemic of seasonally wet sites in the Calvinia district, has unusual brick red flowers with contrasting centre, signalling an adaptation to monkey beetle pollination. Photo: J. Manning

Several years ago *Veld & Flora* published a review of the Cape genus *Sparaxis,* which then included seven species which shared a radially symmetric perianth and distinctive dry, crinkled and long-toothed or torn floral bracts (*Veld & Flora* **65**, 7-9, 1979). Since then our understanding of the Iridaceae (indeed all aspects of plant classification and pollination biology) in southern Africa has increased dramatically. Flowers, we now know, have an important adaptive function. They must ensure the production of a new generation of plants by fertilization of ovules and maturation of seeds. In most plants fertilization must be achieved by persuading an insect, bird or some other agent to visit the flower and transfer pollen from the anthers of one plant or flower to the stigmas of another. Animals that perform this function are called pollinators and they visit flowers for quite selfish reasons, usually to forage on floral products. These products include nectar and pollen, the latter most often collected by female bees to provision their nests. The transfer of pollen is incidental to the pollinator's foraging activity although it is vital to the plant.

Classical *Sparaxis* and two-lipped flowers

In species of *Sparaxis* in the classic sense, that is the common range of garden hybrids and wild species including *Sparaxis tricolor*, *S. elegans* and *S. pillansii*, the flowers fulfil their purpose in a very unusual way. Recent studies conducted by scientists at the National Botanical Institute and the University of Cape Town (see *Veld & Flora* **82**, 17-19, 1996) have demonstrated that flowers of many plants in the winter-rainfall zone of South Africa are used by monkey beetles as the sites for assembly, attraction of mating partners and copulation. The beetles invariably become covered in pollen as they clamber clumsily over a flower, and pollen in turn is brushed off onto stigmas after they move to another flower in search of prospective mates.
The flowers that beetles favour for their activities are often large and brightly coloured, have a flat surface or shallow cup and produce little or no nectar but may produce unusually large amounts of pollen. Very often

these flowers also have contrasting dark markings that, it has been suggested, mimic the beetles themselves as part of a strategy of decoy that may increase the frequency of beetle visits and thus enhance cross pollination. We now believe that the flowers of *S. tricolor*, *S. elegans* and *S. pillansii* are primarily beetle flowers, although they are also visited by small horseflies in search of the traces of nectar that are produced. Some other *Sparaxis* species, including the fairly common south-western Cape *S. grandiflora* appear to have a similar pollination biology but its flowers are also visited by a range of bees that collect pollen.

Another common south-western Cape species, *Sparaxis bulbifera* has a more conventional floral biology. Its cream flowers are cupped and have a hollow floral tube that contains moderate amounts of nectar. They are visited mostly by honey bees and female bees of other species and sometimes by small horseflies in search of nectar, but may also be visited by monkey beetles. Pollen is passively dusted onto the bodies of these insects as they climb into the flowers. Monkey beetle pollination, at least in the Iridaceae, is now understood to be a specialized system and those species of *Sparaxis* with this pollination system are specialized in the genus.

This brings us to *Synnotia*, a small south-western Cape genus now (since 1990) included in *Sparaxis*. *Synnotia* has always been thought to be allied to *Sparaxis* for it has the same specialized floral bracts and the same unusual leaf texture and venation as typical *Sparaxis* species. The only difference between the two genera is that *Synnotia* has highly irregular, two-lipped flowers with an enlarged dorsal tepal, a coloured lower lip, and arched and parallel stamens. Like *Sparaxis bulbifera* these species are mostly pollinated by bees foraging for nectar. Typical examples of the species once included in *Synnotia* are *Sparaxis villosa* from clay soils in the western Cape, and a new species, *S. auriculata* from rocky sandstone slopes in the Vanrhynsdorp district. Floral symmetry alone is not an adequate reason for the recognition of a genus and with the new insight about the adaptive nature of the flowers of some of the typical species of *Sparaxis* we now believe that the species with radially symmetric flowers are actually highly specialized for an unusual pollination system. Moreover, it is apparent from phylogenetic studies of the gene sequences of the genera of the Iridaceae that two-lipped, irregular flowers are the ancestral (or primitive) condition in the Ixioideae, the large subfamily to which *Sparaxis* belongs. Putting this information together, it seems all but certain that *Sparaxis* in the old sense consisted of one or two lineages of highly specialized species derived from an ancestor with the irregular flowers that characterized *Synnotia*. The two genera were united under the older name *Sparaxis* in 1992, which brought the taxonomy of *Sparaxis* back full circle to its original circumscription as defined by the English botanist, John Ker Gawler in 1802, who had actually included species of *Synnotia* in *Sparaxis* when he erected the genus.

The fairly complex, but evidently ancestral, flower type of *Sparaxis auriculata* are visited by bees in search of nectar which the flowers do not produce. The flowers resemble those of *Gladiolus venustus* a favourite nectar source for solitary bees. Photo: J. Manning

Although the flowers of *Sparaxis variegata* resemble those of S. *auriculata*, they do, however, offer ample nectar to long-tongued bees. Photo: J. Manning

Floral diversity and pollination

Today *Sparaxis* includes fifteen species from the south-western Cape and western Karoo all with relatively diverse shapes and pollination strategies. The striking, symmetrical flowers of *S. tricolor* and *S. elegans* are relatively well known to gardeners and we now understand that the brilliant flower colours are actually signals to monkey beetles to visit the flowers. The much less well known *S. villosa*, *S. variegata* and the new species, *S. auriculata* have flowers very like those of the common bee-pollinated *Gladiolus venustus* of the south-western Cape and in fact they share the same species of bees as their pollinators. The bright yellow lower lip is a signal to bees and is often called a nectar guide, while the enlarged dorsal tepal shelters and conceals the pollen so that is it less exposed to the elements and to insects that might take pollen without effecting pollination. Curiously, the display provided by the flowers of *S. auriculata* is pure bluff. Although this species has the largest flowers of any sparaxis it does not produce nectar. The tube is tightly closed and visiting bees are consistently disappointed in their search for nectar on this plant. However, we suspect that bees cannot distinguish these flowers from very similar ones that secrete nectar and so are repeatedly tricked into visiting and pollinating flowers of *S. auriculata*.

The flowers of *S. villosa* do yield nectar, but this species has a failsafe mechanism built into its biology. The flowers have very short styles so that the stigmas are in contact with the pollen. If insect-mediated pollen transfer does not occur, the flowers readily self-pollinate themselves. The nectar then goes to waste, but production of a seed crop for the next year is safeguarded.

Sparaxis metelerkampiae from the lower mountain slopes of the Western Cape has perhaps the most remarkable flowers of any sparaxis. They are dark violet in colour with the lower lip streaked with white or yellow, and have an elongated floral tube up to 30 mm long. The only insects able to reach the nectar produced in the tubes of these flowers are long-proboscid flies (*Prosoeca* spp.) and the flowers of the species are adapted to this specialized pollinator. The flowers resemble another violet-flowered species with a white-streaked lower lip, the common *Laperiousia jacquinii*. This *Lapeirousia* and *S. metelerkampiae* are actually members of a guild of plant species that have darkly pigmented, long-tubed flowers and are all pollinated exclusively by long-proboscid flies. These *Prosoeca* flies are rare today in the area south of Clanwilliam and *L. jacquinii* and *S. metelerkampiae* successfully reproduce in the part of their range south of Clanwilliam only through self-pollination or occasional visits by stray insects that fail to reach the nectar and move to the flowers of other plants. We have yet to learn why *Prosoeca* flies have disappeared from part of their range for they are often common north of Clanwilliam and extend into southern Namibia. There, species pollinated exclusively by long-proboscid *Prosoeca* flies are often (but not invariably) self-sterile and therefore depend entirely on one particular pollinator for their sexual reproduction.

One of the least known species of *Sparaxis* is the diminutive *S. parviflora* which grows in sandy and granitic soils along the Cape west coast from Darling to Hopefield. The flowers are tiny, but are lightly scented and offer minute amounts of nectar. The plants also grow in dense colonies, which makes it worth-while for honeybees to visit them for both nectar and pollen. Despite having this common pollinator, flowers of *S. parviflora* have short stigmas and are also self-fertile. Perhaps in this species the failsafe reproduction strategy is simply inherited from an ancestor with a less reliable pollination system.

Thus despite its relatively few species, *Sparaxis* is a fairly diverse genus in terms of its flower shape. The different species have become adapted to a surprising range of pollinators. These include the apparently ancestral system using antho-phorine bees with nectar as a reward (or with no reward at all), long-proboscid flies, also with nectar as a reward, honeybees with pollen as a reward, more generalist systems involving a range of bees, flies and hopliine beetles, or the highly specialized mokey-beetle and horsefly system. Knowing that flowers have specific functions and that particular flower shapes are adapted for pollination by different organisms, we can look at flowers from a new perspective. They please us with their colour, shape and scent both in the wild and in gardens, but they can also be understood as playing very specific roles in the biology of the plant and in the ecosystems they inhabit.

The highly derived flowers of *Sparaxis metelerkampiae* have a long perianth tube and are pollinated by a long-proboscid fly which is attracted to dark red- or violet-coloured flowers. Photo: J. Manning

About the Authors

Peter Goldblatt is the Curator of African Botany at the Missouri Botanical Garden, St. Louis, Missouri with which he has been associated since 1972, when he left a teaching position at the University of Cape Town, South Africa. Peter has made the study of the Iris family a lifetime research interest and he is one of the world's leading experts on the Iridaceae and its close relatives. Although members of the Iridaceae are world-wide in distri-bution, the family has a marked concentration on the African continent where over 1000 of the estimated 1800 species are native. His research on various genera of the Iridaceae has taken him on numerous field trips to Africa as well as southern Europe, the Middle East, and parts of North America. His travels in the field have been funded by the U. S. National Foundation and the U.S. National Geographic Society. Author of some 200 scientific papers, Peter has also written several books including *The Moraeas of Southern Africa*, *The Genus Watsonia*, *The Woody Iridaceae*, *Gladiolus in Tropical Africa* and most recently *Gladiolus in Southern Africa* in collaboration with John Manning.

John Manning was born in Pieter-maritzburg, and since 1989 has been a Research Scientist with the National Botanical Institute at Kirstenbosch. Although John has studied the anatomy, embry-ology and seed development of diverse plants, including those in families such as the Fabaceae, Proteaceae and Stilbaceae he has focused his research more recently on the Iridaceae, collabo-rating on several different research projects with Peter Goldblatt. Together they have investigated the phylogeny and pollination biology of *Lapeirousia* and subsequently the systematics, pollination systems and evolution of *Gladiolus* in southern Africa. John is an accomplished botanical artist and plant photographer. His drawings have been published in numerous scientific papers, flora treatments and books. His most recent work is *Gladiolus in Southern Africa* in collaboration with Peter Goldblatt.