Systematics and biology of
the Cape genus

SPARAXIS

(Iridaceae)

Peter Goldblatt & John Manning

Strelitzia 32

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Peter Goldblatt and John Manning
South African National Biodiversity Institute

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STRELITZIA

This series has replaced *Memoirs of the Botanical Survey of South Africa* and *Annals of the Kirstenbosch Botanic Gardens*, which SANBI inherited from its predecessor organisations.

The plant genus *Strelitzia* occurs naturally in the eastern parts of southern Africa. It comprises three arborescent species, known as wild bananas, and one or two acaulescent species, known as crane flowers or bird-of-paradise flowers. Part of the logo of the South African National Biodiversity Institute is based on the striking inflorescence of *Strelitzia reginae*, a native of the Eastern Cape and KwaZulu-Natal that has become a garden favourite worldwide. It symbolises the commitment of the Institute to champion the exploration, conservation, sustainable use, appreciation and enjoyment of South Africa's exceptionally rich biodiversity for all people.

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Introduction

One of the smaller genera of subfamily Crocoideae, *Sparaxis* Ker Gawl. is restricted to the southern African winter rainfall area in the southwest of the subcontinent. The genus falls in tribe Ixieae Dumort. (1822) [syn. Croceae Dumort. (1827)]. With the addition of one new species described here, *Sparaxis* now comprises 16 species. In this monograph of the genus we outline the morphology of the species, their floral biology, and their diverse and specialized pollination strategies. Molecular studies using plastid and nuclear DNA sequences have made it possible to infer the more precise relationships of the genus within Ixieae and also to draw some conclusions about the phylogenetic relationships of the species. In the past, historical precedence was maintained in referring zygomorphic-flowered species to sect. *Synnotia* Sweet and those with a symmetric perianth (but sometimes unilateral stamens and style) to sect. *Sparaxis*, but it is now evident that actinomorphic species evolved more than once from zygomorphic ancestors in the genus and that some of the actinomorphic species are not directly related. We propose a more natural, i.e. phylogenetic, classification of the genus. We also outline the taxonomic history of *Sparaxis* before presenting a formal systematic account of the individual species and their distribution, biology, relationships and history.

Species of *Sparaxis* have been used in horticulture for over 200 years, since their advent in gardens in western Europe in the 1780s. *S. tricolor* (Schneev.) Ker Gawl. remains moderately popular in gardens in parts of the world with mild winters, especially those with Mediterranean climates, and both seed selections and hybrids involving *S. tricolor* and several other species have received some horticultural attention. White-flowered *S. bulbifera* (L.) Ker Gawl. is also occasionally grown in gardens and is a useful addition to rock garden landscapes. The species with zygomorphic flowers have elicited virtually no horticultural interest but are as amenable to cultivation as those with radially symmetric flowers. These species are occasionally grown by bulb enthusiasts and have at times been cultivated successfully at Kirstenbosch Botanical Gardens in Cape Town, South Africa.

Morphology

Corm: the underground storage and perennating organ of *Sparaxis* is of the axial type (Goldblatt *et al*. 2006) in which the base of the stem thickens during development to become the new season's corm. The corm itself consists of several internodes with the apical shoot developed adjacent to the flowering stem. Roots are produced from no fixed position on the lower portion of the subglobose to obconic corm body. Corm tunics are of two types. The more common in the genus consists of fine, relative soft, netted fibres and the other of relatively coarse fibres with the vertical members thickened below and resembling claws. The latter type of tunic is restricted to a small group of allied species comprising *S. variegata* (Sweet) Goldblatt & J.C.Manning, *S. villosa* (Burm.f.) N.E.Br. and *S. meterlerkampiae* L.Bolus, as well as *S. caryophyllacea* Goldblatt, which falls in this group in the nuclear gene-based phylogeny but not in the plastid gene-based phylogeny. Thus, coarsely fibrous corm tunics may have evolved only once or independently in two lineages. We favour the first hypothesis and include *S. caryophyllacea* with the *S. variegata*/*villosa* group. Small axillary cormlets are often produced in the axils of the basal leaves and in *S. bulbifera* also in the axils of the cauline leaves.

Leaves: indeterminate in number, the lowermost foliar organs comprise sheathing, bladeless cataphylls that enclose the base of the plant. The foliage leaves with well-developed blades form a tight, two-ranked fan and sometimes one or a few leaves are inserted on the stem above ground level; these invariably smaller than the basal leaves. The vascular tissue of the cataphylls gives rise, as they decay at the end of the growing season, to the fibrous tunics enclosing the corm, and in some species, notably in *Sparaxis galeata* Ker Gawl. and *S. roxburghii* (Baker) Goldblatt, to the collar of persistent fibres enclosing the base of the plant. Conspicuous purple mottling of the lower leaf sheaths and cataphylls is a characteristic of just three species, *S. auriculata* Goldblatt & J.C.Manning, *S. caryophyllacea* and *S. galeata*. The marginal anatomy is of the derived type, lacking a marginal vein and associated subepidermal strand of sclerenchyma, and with columnar epidermal cells with thickened radial walls. This specialized leaf anatomy is shared with several genera of tribe Ixieae, including the closest relatives of *Sparaxis*, *Duthiastrum* M.P.de Vos and *Tritonia* Ker Gawl. (De Vos 1982a; Rudall & Goldblatt 1991; Goldblatt *et al*. 2006). *Dierama* K.Koch and *Ixia* L., often regarded as close allies of *Sparaxis*, have different leaf marginal anatomy with a subepidermal strand of sclerenchyma (in *Ixia* not associated with a marginal vein).

Stem: round in cross-section, stems offer no contribution to the understanding of the genus except for the branching pattern. When plants are branched, branches are either from aerial nodes on the stem (described here as cauline) or exclusively from nodes close to ground level (described here as basal). The distinction is important for example between *S. bulbifera* (branches produced well above ground and with axillary cormlets) and the otherwise often similar *S. grandiflora* (branches ± basal and without axillary cormlets).

Inflorescence: as in most genera of Crocoideae, the inflorescence is a spike; the flowers thus sessile on the spike axis. Flowers are arranged in subsecund fashion when zygomorphic or spirally when the perianth is radially symmetric. Flower number per spike varies to some extent within a species depending on age and growing conditions, but *Sparaxis fragrans* (Jacq.) Ker Gawl. and *S. maculosa* Goldblatt normally have only two or three flowers.

The paired floral bracts subtending each flower are dry, crinkled, and pale or translucent but usually irregularly streaked with dark brown pigment. Bracts of *Sparaxis tricolor* and its allies (sect. *Streptanthera*) are relatively large, and the outer of the pair is ± deltoid with an acute apex, often becoming irregularly torn with age. Bracts among the other species (sect. *Sparaxis*) are cuspidate; the outer having three attenuate cusps and the inner two similar cusps. The cusps in *S. bulbifera* and *S. grandiflora* are especially prominent, dark brown and somewhat twisted. The margins of the bracts, sometimes including the cusps, of *S. fragrans* and *S. maculosa* are irregularly fringed; a feature that immediately distinguishes them in the genus.

Flowers: the perianth consists of a short to long tube and six subequal to markedly unequal tepals. Floral symmetry ranges from radially symmetric with stamens erect and surrounding the style through bilabiate with stamens and style unilateral and with the dorsal tepal largest, usually erect or suberect and the lower three tepals smaller and held closely together, extending horizontally or directed downward and bearing contrasting markings or nectar guides. Perianth tubes are elongate and relatively narrow in several species with bilabiate flowers, especially in those adapted for pollination by long-proboscid flies of the genus *Prosoeca* (Nemestrinidae). The longest tubes, 30–40 mm long, are found in *S. metelerkampiae* (L.Bolus) Goldblatt & J.C.Manning and *S. variegata*, in which long-proboscid fly pollination has been confirmed; followed by *S. roxburghii*, where it is 20–30 mm long and in which pollination remains to be observed. The relatively long tube in *S. auriculata*, ± 18 mm, is deceptive, for the lower part of the tube has thick walls that tightly enclose the style and force the nectar into the middle of the tube where it is accessible to bees with mouthparts up to 10 mm long.

The flowers of *Sparaxis bulbifera* and *S. grandiflora* are intermediate between the radially symmetric and bilabiate types and have subequal tepals in which the outer whorl is slightly larger than the inner, but the style and stamens are unilateral. The stamens are unusual in not being parallel with contiguous anthers, but rather the three filaments are held apart with the anthers facing the centre of the flower.

Flower colour among the zygomorphic species ranges from yellow, usually with purple markings, often most prominent on the dorsal tepal, through predominantly light purple (*Sparaxis roxburghii*) to dark purple with white (sometimes yellow) nectar guides (*S. metelerkampiae*). Tepals, especially those of the outer whorl, are usually flushed with grey mauve, occasionally dark purple on the outside. Flowers of *S. grandiflora* subsp. *grandiflora* are a remarkable, intense plum-purple colour with a white throat and those of subsp. *fimbriata* (Lam.) Goldblatt and *S. bulbifera* are most often white or almost so but with a yellow throat and often dark spots at the tepal bases. *S. grandiflora* subsp. *acutiloba* Goldblatt has flowers of a deep, clear yellow colour. Most strikingly pigmented of all are *S. tricolor* and its allies from the Bokkeveld Mountains and the Calvinia District. *S. tricolor* has an orange perianth with the yellow centre surrounded with broad, heart-shaped, almost black marks at the tepal bases, and *S. pillansii* L.Bolus has pink to old-rose tepals also with a yellow centre outlined in a dark colour. Most remarkable of all is *S. elegans* (Sweet) Goldblatt, in which the perianth is either salmon-pink or white with a band of dark purple markings, often with a central yellow spot just above the tepal bases.

The flowers of species with a radially symmetric perianth close at night, as do those of *Sparaxis parviflora* (G.J.Lewis) Goldblatt. Species with large, zygomorphic flowers remain open, but the dorsal tepal usually arches forward, thus protecting the stamens and style branches from the elements.

Androecium: the three stamens, arising opposite the outer tepals, have slender filaments inserted just above the base of the anthers (thus subbasifixed). The anthers are developmentally extrorse in dehiscence, but in species with zygomorphic flowers and thus unilateral stamens, the mature anthers face the centre of the flower. Pollen is conventionally coloured yellow to white except in *Sparaxis elegans*, which has dark purple to brown pollen, possibly for the purpose of camouflage as pollen is not offered as a pollinator reward in this species. Anthers are straight except in *S. elegans*, which has S-shaped anthers coiled around the style, and the anthers may be slightly twisted in *S. pillansii*. Pollen structure conforms to the plesiomorphic type for Crocoideae, having a monosulcate aperture with a two-banded operculum (at least in those species examined) and perforate exine with minute supratectal spinules (Goldblatt *et al*. 1991).

Gynoecium: the inferior ovary is ovoid, round in section and uniform across the genus. The slender style divides beyond the perianth tube into three branches, these usually slender and minutely ciliate on the stigmatic surfaces. The level of style division is usually opposite the apex of the anthers or shortly beyond them, but in *S. metelerkampiae* the style divides at the top of the filaments or opposite the bases of the anthers. The species is facultatively autogamous and self-pollination is readily effected by the close proximity of anthers and stigmatic surfaces. The short style in *S. tricolor* and *S. pillansii* also allows for self-pollination when cross pollination fails. Both these last two species as well as *S. elegans* have relatively short style branches somewhat expanded at the tips, particularly broad in *S. elegans*.

Fruit and seeds: the capsular fruits are generally unremarkable, more-or-less cartilaginous and splitting soon after drying to passively release seeds that accumulate on the ground around plants. Capsules are mostly somewhat barrel-shaped with a rounded apex and bulge unevenly, showing the outline of the seeds. Capsules of *Sparaxis maculosa* are unusually globose and do not split open along the locules as in other species, but rather the walls fragment irregularly, releasing the seeds as they decay.

Seeds are globose, hard, shiny and completely smooth, the result of the obliteration of the outlines of the epidermal cells during seed maturation. *Sparaxis* falls in the clade of tribe Ixieae in which the vascular trace to the ovule is excluded during development, a process described in detail elsewhere (Goldblatt *et al*. 2006). Seed size and number vary considerably among the species. The number of seeds per locule ranges from 10–12 in *S. metelerkampiae* down to only 4 in *S. variegata* and a maximum of 6 in *S. parviflora*, which, although it has the smallest flowers in the genus, also has the largest seeds 2.4–2.8 mm in diameter. Seeds in other species range from 1.7–2.2 mm in diameter. (Note: ripe seeds were measured within six months of maturation—older seeds will normally be somewhat smaller due to shrinking following continued dehydration.)

Chromosome cytology: basic chromosome number in *Sparaxis* is $x = 10$ (Goldblatt 1971; Goldblatt & Takei 1997). Ten of the 11 species counted are diploid, with $2n = 20$, but the one population of *S. parviflora* examined is tetraploid, $2n = 40$. Uncounted species are *S. auriculata*, *S. calcicola*, *S. maculosa*, *S. roxburghii* and *S. variegata* [the count in the literature for this species (Goldblatt 1971) is for what is now *S. metelerkampiae*]. Karyotypes are uniform and consist of relatively small chromosomes 1.5–3.0 μm long. Two pairs of somewhat larger, subacrocentric chromosomes are evident; one of which bears a small satellite. The remaining eight pairs are submetacentric to metacentric but too small to characterize accurately.

Among the genera most closely related to *Sparaxis*, *Dierama*, *Duthieastrum* and *Ixia* also have $x = 10$ and comparable karyotypes. That the chromosomes of *Sparaxis* are slightly smaller than those of *Dierama* and *Ixia* (Goldblatt 1971; De Vos 1974) is probably not significant taxonomically. *Tritonia*, also closely related to *Sparaxis*, has $x = 11$ in most of those species that have been counted, but two have $x = 10$ (Goldblatt 1971; De Vos 1982b).

Floral biology and pollination

Sparaxis, like most genera of subfamily Crocoideae, has a diverse floral biology, but this is especially noteworthy given its small size. Most species of sect. *Sparaxis* have the ancestral pollination system of the subfamily in which large bodied, long-tongued anthophorine bees passively transfer pollen while foraging for nectar (Goldblatt & Manning 2006). In these species the nectar reward is of moderate sugar concentration. Three species, *S. fragrans, S. parviflora* and *S. villosa*, are facultatively autogamous but often receive visits by anthophorine bees, specifically honeybees, *Apis mellifera*, in the case of *S. parviflora* (Table 1). Greenhouse exclusion experiments show that all three species produce full capsules of viable seeds. *S. caryophyllacea* and *S. galeata*, both of which have strongly fragrant flowers, have the same pollination system but *S. caryophyllacea*, although self-compatible, is facultatively outcrossing because the stigmatic surfaces do not normally make contact with the pollen, while *S. galeata* is self-incompatible, thus an obligate outcrosser. *S. auriculata* and *S. calcicola* have the same pollination system, but compatibility relations in these two species are not known. Preliminary observations made by Goldblatt *et al*. (2000) indicated that *S. galeata* did not produce nectar, and pollination by deception was postulated for the species, but this is now known to be mistaken. A second population that we examined, from the Kobee Valley, shows that flowers produce ample nectar.

The three long-tubed species, *Sparaxis metelerkampiae*, *S. roxburghii* and *S. variegata*, have flowers adapted for pollination by long-proboscid flies, almost certainly *Prosoeca peringueyi* (Nemestrinidae); the only long-proboscid fly that is on the wing in the Olifants River Valley and nearby when these species bloom. Pollination by this fly has been confirmed for *S. metelerkampiae* and *S. variegata* (Goldblatt *et al*. 2000; Goldblatt & Manning 2006). *S. variegata* is self-incompatible and thus depends entirely on *P. peringueyi* for pollination, whereas *S. metelerkampiae* is facultatively outcrossing—although flowers are frequently visited by the same long-proboscid fly, selfing occurs in the absence of active pollen transfer. Its wider distribution, entirely encompassing the range of *S. variegata*, may be the result of this failsafe mechanism, ensuring ample seed production in the absence of pollinating insects. Compatibility relations and pollination in *S. roxburghii* have not been established.

Pollen may be a secondary reward in some species, and is accumulated in pollen baskets of visiting anthophorine visitors and in the corbiculae of *Apis* workers. The latter were reported by Goldblatt *et al*. (2000) to be actively collecting pollen from *Sparaxis parviflora*.

In sect. *Sparaxis* generalist pollination has been found in *S. bulbifera*, *S. fragrans* and *S. grandiflora* subspp. *fimbriata* and *acutiloba*, in which halictid bees, *Apis mellifera* workers, various Diptera, and hopliine beetles have all been recorded visiting and pollinating the flowers (Goldblatt *et al*. 2000). The only pollinator noted to date on the deep purple flowers of *S. grandiflora* subsp. *grandiflora* is the hopliine beetle, *Peritrichia rufotibialis*. Hopliine pollination has also been established for *S. elegans*, *S. pillansii* and *S. tricolor*, but the tabanid fly, *Philoliche atricornis*, also visits flowers of all three species, probably in search of minute traces of nectar. Both the tabanid flies and hopliine beetles carry large quantities of host flower pollen and are effective pollinators of all three species, which may thus be regarded as having bimodal pollination systems (sensu Manning & Goldblatt 2005) in exploiting visitors from two different pollinator groups. On balance, however, we regard the pollination of these species as hopliine dominated. The significance of another visitor to flowers of *S. pillansii*, small empidid flies (Empididae), remains to be established, but numerous individuals of

Table 1.—Compatibility relations, pollination system and nectar characteristics in *Sparaxis*: s-c self-compatible; s-i, self-incompatible. Nectar concentration figures represent % sucrose equivalents

Species	**Compatibility relations**	**Breeding system**	**Pollination system**	**Nectar volume** µl	**Nectar concentration**
auriculata	unknown	unknown	anthophorine bee	0.8–1.2	40.5 (SD 1.0)
bulbifera	s-c herkogamous	facultative outcrosser	generalist, mainly large bees	1.2–1.8	38.0 (SD 3.2)
calcicola	infer s-c herkogamous	unknown	large bees	1.0–1.5	29.5% (SD 2.2)
caryophyllacea	s-c, herkogamous	facultative outcrosser	anthophorine bee	0.8–1.6	26.1 (SD 2.8)
elegans	s-c	facultative outcrosser	hopliine beetle, tabanid fly	trace	unknown
fragrans	s-c	facultative outcrosser	generalist (small bees, flies, hopliines)	trace	unknown
galeata	s-i	obligate outcrosser	anthophorine bee	1.0–1.5	31.7% (SD 3.2)
grandiflora	s-c, often herkogamous	facultative outcrosser	generalist or hopliine beetle	trace	unknown
maculosa	unknown	infer facultative outcrosser	hopliine beetles (inferred)	unknown	unknown
metelerkampiae	s-c	facultative outcrosser	long-proboscid fly	1.4–3.9	25.8 (SD 1.9)
parviflora	s-c	facultative outcrosser	honey bee	trace	unknown
pillansii	s-c	facultative outcrosser	hopliine beetle, tabanid and ?empidid flies	trace	unknown
roxburghii	unknown	unknown	long-proboscid fly (inferred)	1.3–1.8	29.3 (SD 1.5)
tricolor	s-c	facultative outcrosser	hopliine beetle, tabanid fly	trace	unknown
variegata	s-i, herkogamous	obligate outcrosser	long-proboscid fly	1.2–2.4	28.2 (SD 1.3)
villosa	s-c	facultative outcrosser	anthophorine bee	1.1–1.5	24.3 (SD 2.0)

these small insects are regularly observed in open flowers. These active insects carry visible quantities of the pale pollen of *S. pillansii* on the dorsal parts of their bodies. Little is known about pollination by empidid flies, but they are reported to be effective pollinators of some Northern Hemisphere plant species (Proctor *et al*. 1996), mostly with rather inconspicuous flowers. We have also been repeatedly struck by the presence of these small insects, ± 3 mm long, in flowers of *Ixia rapunculoides* Delile (Goldblatt & Manning 2011), always covered with dorsal deposits of its pollen. For the empidids to be significant pollinators, they would need to move from flowers of one plant to another and we have not recorded information on this aspect of their behaviour.

Pollination and compatibility relations remain to be established for *Sparaxis maculosa* and *S. grandiflora* subsp. *violacea*. Hopliine pollination seems likely for *S. maculosa* in light of its bowl-shaped, odourless flower with a dark centre. Subsp. *violacea*, however, has strongly scented flowers, suggesting pollination by anthophorine bees. Its delightful, freesia-like scent is always associated with pollination by large bees in other genera, notably *Gladiolus* and *Freesia*.

Nectar, the primary reward for pollinating insects in most species, is sucrose dominant in *Sparaxis bulbifera* and *S. metelerkampiae* (the only two species examined for nectar chemistry). Sugar concentrations are relatively high in bee pollinated *S. auriculata* (mean 40.5%) and *S. bulbifera* (38%) but lower in *S. caryophyllacea* (26.1%) and the facultatively outcrossing *S. villosa* (24.3%), which has the lowest nectar concentration so far recorded for the genus. The long-proboscid fly pollinated species have intermediate nectar concentrations: *S. metelerkampiae* (28.5% and 25.8% in two separate populations), *S. roxburghii* (29.3%), and *S. variegata* (28.2%). Nectar volumes are highest in long-proboscid fly pollinated species, ranging from a maximum of 3.9 μl in *S. metelerkampiae* to a low of 1.8 μl in *S. roxburghii*. Bee pollinated species and generalists have volumes ranging from 1.2 μl in *S. auriculata* to 1.8 μl in *S. bulbifera*.

Nectar, not until now analyzed for *Sparaxis calcicola* or *S. galeata*, conforms to these patterns. Nectar volume ranges from 1.0 to 1.5 μl in both species, with a mean concentration of 29.5% (SD 2.2, n = 5) sucrose equivalents in *S. calcicola* and 31.7% (SD 3.2, n = 5) in *S. galeata*, thus in the usual range for bee pollinated species.

Pollen may be a secondary reward as it is accumulated in pollen baskets of anthophorine visitors or corbiculae of *Apis* workers. The latter were reported by Goldblatt *et al.* (2000) to be actively collecting pollen from *Sparaxis parviflora* and some captured bees carried only *S. parviflora* pollen. The sole reward for hopliine beetles is a platform on which to assemble, engage in competitive behaviour, select mates and copulate (Goldblatt *et al.* 1998; Steiner 1998).

Sparaxis shows surprising variation in compatibility relations. Two species, *S. galeata* and *S. variegata*, are self-incompatible, obligate outcrossers, but *S. caryophyllacea*, which is self-compatible, is an outcrosser due to herkogamy: the stigmatic surfaces are held well apart from the pollen-bearing anthers. In contrast, *S. fragrans* (a generalist), *S. metelerkampiae* (long-proboscid fly pollinated), *S. parviflora* (honey bee pollinated) and *S. villosa* (anthophorine bee pollinated) are facultatively autogamous. When pollinators are excluded, all three species produce full capsules of viable seeds (Goldblatt 1992). We infer the same breeding system for *S. roxburghii*, which also has a short style with the style branches reaching the lower halves of the anthers. The pattern in *S. metelerkampiae* parallels that in many species of Iridaceae with specialized pollination systems in developing a failsafe mechanism in case their sole pollinator is absent (Goldblatt & Manning 2006). Thus facultative autogamy is recorded in long-proboscid fly pollinated *Babiana tubiflora* (L.f.) Ker Gawl., *Lapeirousia anceps* (L.f.) Ker Gawl. and *L. oreogena* Goldblatt, bird pollinated *Babiana ringens* (L.) Ker Gawl. and *B. aviceps* Goldblatt & J.C.Manning, and moth pollinated *Gladiolus tristis* L. Species of these genera are typically obligate outcrossers.

A third compatibility pattern has been described for *Sparaxis bulbifera*, *S. grandiflora* (which subspecies not known) and *S. tricolor* by Horn (1962). All three can readily be selfed, but in the absence of active pollen transfer autogamy results in the production of a reduced number of capsules. Horn's pooled results for the three species showed that 28.6% of flowers spontaneously selfed and produced capsules versus 47.8% in hand-selfed flowers. In contrast, in open pollinated crosses 82.7% of flowers set seed. The number of seeds produced in open pollinated flowers (mean 10.7) differed from results with spontaneous (mean 14.5) or artificial selfings (mean 10.5). These observations are less useful because results for individual species were not reported separately. Nor do we know the number of seeds produced by these species in the wild. Horn noted that all three of the species were cross compatible. The pattern described by Horn evidently matches the situation in *S. caryophyllacea*, where spatial separation of stigmatic surfaces and pollen account for poor seed set in self-compatible pollinations. This is likely to be the case for *S. bulbifera* and *S. grandiflora*, in both of which the anthers are not in immediate contact with the style branches. We suspect that autogamous pollinations in *S. tricolor* will result in a high percentage of successful crosses because the style branches are held close to the anthers.

Sparaxis species are interfertile (Horn 1962; Horn & Bundies 1989) and interspecific hybrids have been produced between the three species of the *S. tricolor* group as well as between *S. grandiflora* and *S. elegans*, thus between species of separate sections according to our classification.

Comparing pollination systems on the phylogenetic tree (Figure 1b) of *Sparaxis* leads us to conclude that large-bodied anthophorine bee pollination by *Anthophora* and *Amegilla* spp. is ancestral in the genus, being present in all main clades including *S. caryophyllacea*, sister to the *S. tricolor* clade. The three species of the latter clade have short-tubed, radially symmetric flowers that have a hopliine beetle dominated pollination system also using the short-proboscid tabanid fly, *Philoliche atricornis*. In the *S. grandiflora* clade, *S. bulbifera* and *S. grandiflora* have evolved radial floral symmetry and a mixed pollination strategy, but probably dominated by hopliine beetles in *S. grandiflora*. Within this species, subsp. *grandiflora* appears to have shifted to exclusive hopliine pollination. Long-proboscid fly pollination evolved in *S. variegata* and *S. metelerkampiae*, associated in this last species with self-compatibility. Long-proboscid fly pollination is also inferred for *S. roxburghii*, sister to bee pollinated *S. auriculata*. We infer hopliine beetle pollination for *S. maculosa*, sister to the generalist *S. fragrans*.

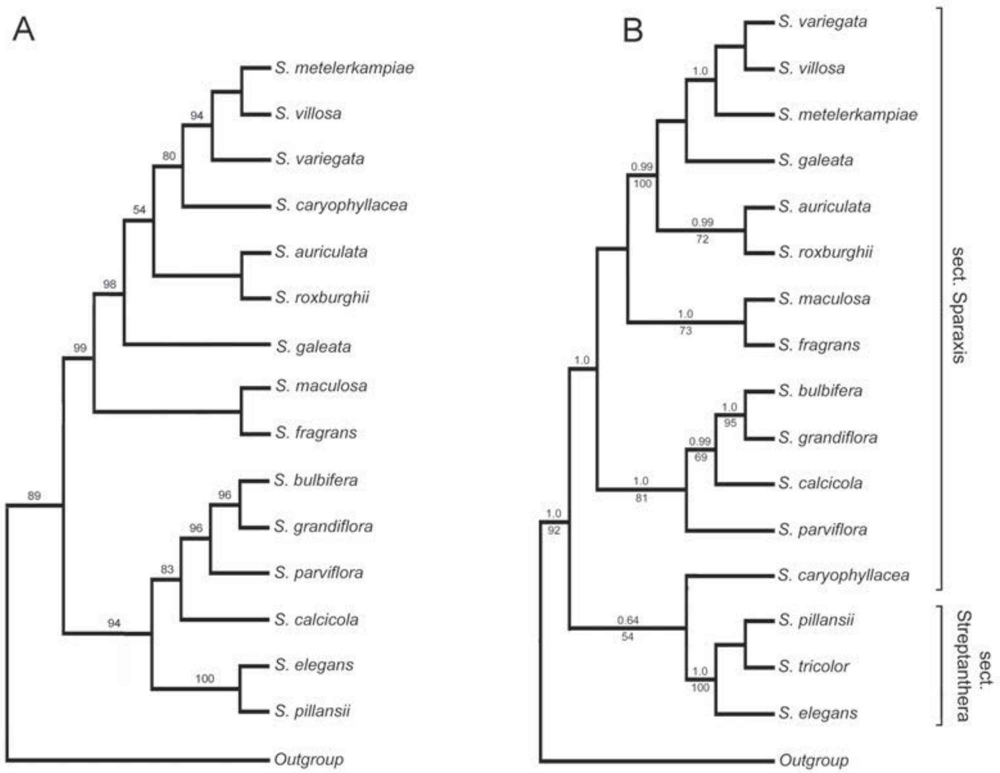
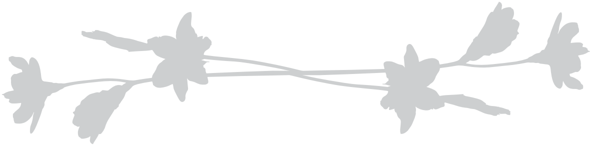


FIGURE 1.—Phylogenetic relationships in *Sparaxis*. A, Maximum Likelihood tree for the nuclear locus *RPB2*; B, Majority Rule Consensus of 5 000 trees received after burn-in of Bayesian analysis of combined plastid loci trnQ-5'rps16, rpl32-trnL and 3'trnV-ndhC, and the nuclear locus *RPB2*. Branch posterior probabilities are shown above and MP bootstrap below (values < 50% are not shown). *Babiana ringens*, *Duthiastrum linifolium*/(E.Phillips) M.P.de Vos, *Ixia latifolia* D.Delaroche and *Tritonia disticha* Baker were used as the outgroup (Modified from Tang 2009).

Thus in this small genus pollination strategies are extremely labile. Long-proboscid fly pollination evidently arose twice, a generalist strategy also twice, and hopliine pollination or hopliine dominated pollination three times if we consider *S. grandiflora* subsp. *grandiflora* as having a system different from the other subspecies of *S. grandiflora*.



Geography and conservation status

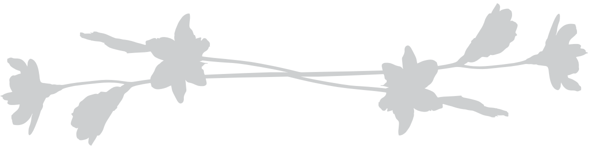
A genus endemic to the winter-rainfall zone of southern Africa (the Greater Cape Floristic Region), *Sparaxis* is restricted to the western half of Western Cape (in the Core Cape Floristic Region) and the extreme southwestern limits of Northern Cape on the Hantam plateau. Most species have narrow ranges, with some known from one or a few small populations. *S. maculosa* is restricted to a few hectares near Stettyn, north of Villiersdorp and *S. roxburghii* to an area of less than one hectare on a single farm in the Olifants River Valley north of Citrusdal, where we estimate the population to comprise less than 100 individuals. *S. caryophyllacea* is similarly known from a single small population on the slopes of the Nardouw Mountains north of Clanwilliam. Because of their narrow ranges, small population sizes, and vulnerability to disturbance, all three of these species must be regarded as Critically Rare, thus with CR status (Raimondo *et al*. 2009) (Table 2). *S. tricolor* is known from three sites on the Bokkeveld Escarpment near Nieuwoudtville; two of them degraded and becoming overgrown with alien species, mostly grasses. Raimondo *et al*. (2009) accorded the species VU (Vulnerable) status, but we suggest this be revised to EN (Endangered). *S. auriculata* is known from a few sites in the Gifberg Mountains, all in undisturbed vegetation, and is listed as EN (Endangered) by Raimondo *et al*. (2009). The Western Karoo species, *S. pillansii*, is relatively widespread in the Calvinia District of Northern Cape, and although none of the several populations is currently under any stress, their small size renders them vulnerable to minor changes in land use patterns. The species is rated as R (Rare) (Raimondo *et al*.

Table 2.—Conservation status for species of *Sparaxis*. Data taken from Raimondo *et al*. (2009) with suggested changes resulting from our experience in the field. We suggest conservation status for those species new in this account. Key: CR, Critically Rare; EN, Endangered; VU, Vulnerable; NT, Near Threatened; R, Rare, no direct or potential threat

Species	**Raimondo *et al*. conservation status**	**Suggested change**	**Species**	**Raimondo *et al*. conservation status**	**Suggested change**
S. auriculata	EN	-	*S. grandiflora* subsp. *violacea*	LC	VU or EN
S. bulbifera	LC	-	*S. maculosa*	CR	-
S. calcicola	-	R	*S. metelerkampiae*	LC	?VU
S. caryophyllacea	CR	-	*S. parviflora*	NT	VU or EN
S. elegans	VU	-	*S. pillansii*	R	?LC
S. fragrans	VU	EN	*S. roxburghii*	CR	EN
S. galeata	VU	-	*S. tricolor*	VU	EN
S. grandiflora subsp. *acutiloba*	LC	VU	*S.variegata*	VU	-
S. grandiflora subsp. fimbriata	LC	NT	*S. villosa*	LC	-
S. grandiflora subsp. grandiflora	EN	-			

2009). The discovery in 2013 of extensive populations of *S. pillansii* on the Farms Tierhoek and Wilgebosch near Calvinia suggest a possible status of LC (Least Concern) for the species. The range of the western coastal *S. parviflora* has been significantly reduced in the past 25 years as urban development has expanded, notably in the Saldanha–Vredenburg area, and we consider the species as VU (Vulnerable), rather than NT (Near Threatened).

The more widespread *Sparaxis bulbifera*, *S. metelerkampiae* and *S. villosa* have all lost some range, but we agree with Raimondo *et al*. (2009) that they merit LC (Least Concern) status (Table 2). We disagree, however, with LC (Least Concern) status for *S. variegata*, which like its VU (Vulnerable) relative *S. galeata*, has an equally narrow range in similar habitats. The Caledon District endemic, *S. fragrans*, also accorded VU (Vulnerable) status, has lost much of its range through agricultural expansion plus the reprehensible policy of spraying weed-killer along road verges, and we suggest EN (Endangered) status is more appropriate. Likewise, *S. grandiflora* subsp. *violacea*, also restricted to the Caledon District, has lost much of its range in the past 25 years and VU (Vulnerable) or even EN (Endangered) status is more appropriate than the current LC (Least Concern). The range of *S. elegans* is now known to extend from north of Nieuwoudtville southward to the Klein Kobee. Although most populations are virtually intact and disturbed only by moderate to heavy grazing, many are highly vulnerable to overgrazing or agricultural disturbance, and the current status of VU (Vulnerable) is appropriate. In the species accounts that follow, conservation status as recommended by Raimondo *et al*. (2009) is listed, with our revised recommendation if we consider that necessary.



Phylogeny and infrageneric classification

The immediate relationships of *Sparaxis* in the narrow sense (i.e. those species with radially symmetrical flowers) have always been thought to lie with the broadly similar genera *Ixia* and *Tritonia* and with *Dierama*, which has superficially similar floral bracts. Lewis (1954), for example, included these four genera plus *Chasmanthe* N.E.Br., *Crocosmia* Planch., *Geissorrhiza* Ker Gawl., *Gladiolus*, *Hesperantha* Ker Gawl. and *Melasphaerula* (together with immediately related *Streptanthera* and *Synnotia*) in her subtribe Ixiinae. Goldblatt (1991) maintained this classification but treated the group as tribe Ixieae, in which also he included *Duthiastrum*, described by M.P. de Vos (1974 as *Duthiella*). Lewis's evolutionary tree placed *Synnotia* at the terminus of the branch that included *Sparaxis* and *Streptanthera*, with that branch closest to one leading to *Tritonia* and its presumed allies, *Chasmanthe* and *Crocosmia* (plus the monospecific *Curtonus* N.E.Br. and *Montbretiopsis* L.Bolus, both now synonymized). The presumption, not specifically stated, was that floral radial symmetry was always ancestral to bilateral symmetry.

Prior to the time of Lewis's work, the genus *Synnotia* (i.e. the species with zygomorphic flowers) had seldom been associated with *Sparaxis*. Baker (1877 and later) included *Sparaxis* and *Streptanthera* in his major infrafamilial group 'series' Ixieae but placed *Synnotia* in 'series' Gladioleae. In similar vein, Klatt (1882) placed *Sparaxis* and *Streptanthera* in his tribe Ixieae whereas he regarded *Synnotia* as a member of tribe Gladioleae. Both authors were clearly influenced by the perceived significance of floral symmetry. In Pax's (1882) account of the Iridaceae for *Die Natürlichen Pflanzenfamilien*, however, we find for the first time since Ker Gawler described *Sparaxis*, both it and *Synnotia* residing in the same tribe, Gladiolieae; inexplicably, however, *Streptanthera* remained in Ixieae.

The pervasive belief that radial symmetry always precedes bilateral symmetry in evolution led Goldblatt (1992), in the first cladistic analysis of the genus, to treat both *Sparaxis* and his chosen outgroup, *Tritonia*, as having radially symmetric flowers as the ancestral condition (one species of *Tritonia* has a radially symmetric flower and three more have a radially symmetric perianth but unilateral stamens and style). His analysis produced a tree with *Sparaxis tricolor* and its close allies as sister to the rest of the genus. In turn, *S. fragrans*/*S. maculosa* with radially symmetric flowers were retrieved as sister to the remaining species. In the resulting classification all species with a radially symmetric perianth or fully actinomorphic flowers were referred to sect. *Sparaxis*, and the remainder, all with bilaterally symmetric flowers with parallel stamens, to sect. *Synnotia*. In a second cladistic analysis, Goldblatt *et al*. (2000) treated the outgroup, still *Tritonia*, as having an ancestrally zygomorphic flower (a correct decision in light of later molecular phylogenetic analysis). This resulted in a very different tree, with species of sect. *Synnotia* now sister to sect. *Sparaxis* plus *S. parviflora*.

Molecular studies using plastid DNA sequences (Reeves *et al*. 2001; Goldblatt *et al*. 2006) have confirmed the close relationship of *Sparaxis* to *Tritonia*. The second of these two analyses, using five plastid DNA regions from a single species of each genus of subfamily Crocoideae, placed *Sparaxis* plus *Duthiastrum* as sister to *Dierama* plus *Ixia*/*Tritonia* (BP 81%). The association of *Sparaxis* and *Duthiastrum* received bootstrap support of less than 50%, evidently dispelling any suggestion that the two genera are so closely allied that they could be regarded as a single genus. We note a caveat here: the addition of more species of *Tritonia* (± 30 spp.) in molecular analyses together with these two genera may alter this scenario—it remains possible that *Duthiastrum* is nested in *Tritonia*.

A molecular-based phylogenetic study of *Sparaxis* (Tang 2009) using DNA sequences of one nuclear and three plastid loci from a single population sample of each species has now dispelled some of the remaining questions about both the relationships of the genus and its phylogeny (Figure 1). *Sparaxis* plus *Synnotia* are a clade, sister to the combined outgroup consisting of a species each of *Babiana*, *Duthiastrum*, *Ixia* and *Tritonia* (or in the nuclear gene-based phylogeny sister to *Duthiastrum* alone) and are appropriately regarded as a single genus.

Unfortunately, relationships within *Sparaxis* are still incompletely resolved, with several significant incongruencies between the nuclear and plastid gene-based phylogenies. Both analyses do, however, consistently associate the members of the *S. tricolor* alliance, which are morphologically united by their distinctive bracts and brightly coloured, radially symmetric flowers. Most analyses also associate the members of the *S. villosa* group, which share heavily thickened corm tunics. It seems likely, therefore, that these two groups of species represent natural alliances.

One of the most striking of the incongruencies is the placement of *Sparaxis caryophyllacea* in the plastid (and combined) analysis (Figure 1b) as sister to the *S. tricolor* group, with which it shares no morphological synapomorphies, and in contrast to its association with the *S. villosa* group in the nuclear analysis (Figure 1a). This latter grouping is apparently supported by the shared development of woody corm tunics in the group. We note that in the combined tree the position of *S. caryophyllacea* is without statistcal support. The nuclear gene-based phylogeny retrieves *S. fragrans* and *S. maculosa* as sister species, which is consistent with their several morphological similarities, notably their diagnostic, laterally fringed bracts and radially symmetric flower. This topology is also retrieved in the combined tree but not in the plastid analysis (not shown), which separates the two species, allying *S. maculosa* with *S. bulbifera* and *S. grandiflora* but linking *S. fragrans* with *S. roxburghii*/*S. auriculata*/*S. parviflora*. Not surprisingly, *S. bulbifera* and *S. grandiflora* are retrieved as sister species in all analyses, and in both the nuclear and combined analyses the species pair comprise a clade with *S. calcicola* and *S. parviflora*. Morphology offers no insight into this association, but it is important to stress that in all analyses *S. bulbifera* and *S. grandiflora* (perianth but not stamens radially symmetric) are nested among species with fully zygomorphic flowers. All analyses also link *S. auriculata* and *S. roxburghii* as immediately allied; an association neither supported nor refuted by morphology. Beyond this, however, it is not possible to infer anything more meaningful about relationships among the species using the available molecular data. We note, however, that the nuclear gene-based analysis seems to us to provide a stronger phylogenetic signal that is more congruent with morphology in the position of *S. caryophyllacea*.

Although the molecular phylogenetic data are not consistently robust enough for us to infer all phylogenetic relationships among the species, there is no doubt that the *S. tricolor* group is a monophyletic lineage that is also well diagnosed morphologically. Morphology suggests no obvious allies and it evidently represents an early-diverging lineage in the genus. A dated phylogeny, or chronogram, for the genus developed by Tang (2009) estimates its divergence from the last common ancestor at 3.6 mya, relatively shortly after the origin of the genus, estimated at 4.3 mya. We therefore segregate the *S. tricolor* group from the rest of the genus as sect. *Streptanthera* to underline its phylogenetic and morphological distance (as noted above, the position of *S. caryophyllacea* as sister to the *S. tricolor* group in the combined analysis (Figure 1b) lacks statistical support and is morphologically anomalous). We follow the nuclear analysis (Figure 1a) for our taxonomic treatment in placing *S. caryophyllacea* close to *S. villosa* and its allies, with which it shares woody corm tunics. We treat this second, larger section of the genus as sect. *Sparaxis*. Possible morphological synapomorphies for the group include the lacerate bracts, but the zygomorphic flower may be ancestral in the genus: radial symmetry of the perianth or stamens is then interpreted as a secondarily specialization.

Based on the combined analysis of plastid and nuclear gene regions, there can be no doubt that radial floral symmetry of the perianth has evolved at least twice in *Sparaxis* and probably three times, once in the ancestor to the *S. tricolor* group and either separately in the ancestors of the *S. fragrans*/*S. maculosa* and *S. grandiflora*/*S. bulbifera* species pairs or possibly once if these four species are found ultimately to comprise a single clade. This interpretation receives independent morphological support from differences in bracts and stamen arrangement in the three groups. Such evolutionary lability in floral organization is remarkable in a genus of flowering plants, although not unprecedented. Even within the African Iridaceae, floral radial symmetry has evolved at least four times in *Gladiolus* L. (Goldblatt 1989, 1996; Goldblatt & Manning 1998), but with over 250 spp. in sub-Saharan Africa and Madagascar, this is a far lower frequency than in *Sparaxis*. The evolutionary history of the hardened, claw-like tunics is less clear. The nuclear analysis suggests a single evolutionary event whereas the plastid (and combined) tree indicates two separate events, once in *S. caryophyllacea* and again in the *S. villosa* group. The most parsimonious interpretation of morphological characters favours the single evolutionary event.

The application of molecular dating methods to the generic phylogeny of Iridaceae, Goldblatt *et al*. (2008) suggest that *Sparaxis* plus its sister genus *Duthiastrum* may have diverged from a clade including *Dierama*, *Ixia* and *Tritonia* in the mid Miocene, ± 15 mya (much earlier than Tang's (2009) estimate which included only *Sparaxis* and immediately related genera). This coincides with the major generic radiation of subfam. Crocoideae (Goldblatt *et al*. 2006) at about the time of renewed glaciation in Antarctica, which led to a drop in ocean temperatures and intensification of the south Atlantic high pressure cell (Zachos *et al*. 2001). A major climatic result of this oceanic cooling was the increasing desiccation of the western half of southern Africa and an intensification of summer drought, leading ultimately to the development of the winter-rainfall climate that prevails there today.

Speciation

Determinants of speciation are complex, often involving factors like geography, soil preferences and associated vegetation and, in the case of *Sparaxis*, pollinators. Comparison of the molecular phylogeny (Figure 1, Table 3) with morphology allows us to infer likely drivers of speciation for several species. Both geography and pollinators appear to have been involved in stimulating the divergence of the *S. tricolor* group. These species have shifted from the ancestral pollination system of fragrant, nectar-producing flowers pollinated by large-bodied anthophorine bees to a hopliine beetle-dominated system, with an associated shift to radial floral symmetry, the development of bright pigmentation with sharp colour contrasts, and a loss of floral fragrance. The *S. tricolor* group is geographically isolated along the dry, northern margins of the Cape Floristic Region from the rest of the genus. Within the group, small soil differences appear to have been important in driving the diversification: the species pair *S. tricolor* and *S. pillansii* both favour seasonally moist situations, but the former grows on sandstone-derived soils and the latter heavy clay most often derived from dolerite.

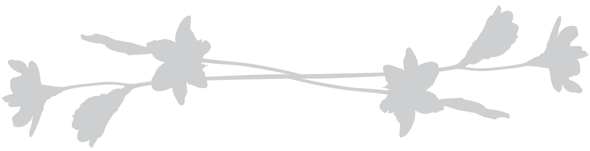
The species pair *S. bulbifera* and *S. grandiflora* are also separated only by different soil preferences, sandy or clay habitats respectively. *S. calcicola* is unique in being endemic to limestone of lime-enriched habitats; its likely closest relative may be the facultatively autogamous *S. parviflora*, which tiny flowers are sometimes visited by *Apis mellifera*. The subspecies of *S. grandiflora* all appear to be geographic isolates, but with an evident shift to exclusive hopliine pollination in subsp. *grandiflora* and a likely shift to pollination dominated by large-bodied bees in subsp. *violacea*, given its highly fragrant flowers. The species pair *S. auriculata* and *S. roxburghii* are local endemics with similar habitat preferences that are geographically isolated by a fair distance and *S. roxburghii* also shows a pollinator shift (inferred) to long-proboscid flies. *S. fragrans* and *S. maculosa*, also geographic isolates, share a similar habitat, and if our inference is correct that the latter is adapted for pollination by hopliine beetles, then this represents a shift from the generalist pattern (including hopliines) in *S. fragrans* or vice versa. Lastly, *S. variegata* and *S. metelerkampiae* have similarly specialized flowers for long-proboscid fly pollination, and despite weak support for their immediate relationship from the molecular phylogeny (Figure 1a), we see them as sister species. They are parapatric and evidently share similar stony, sandstone derived soils but never co-occur. *S. variegata* is usually found in drier situations and is self-incompatible whereas *S. metelerkampiae*, which has smaller flowers, is facultatively autogamous.

In summary, available data suggests that speciation in the genus was driven by a mix of factors, including geographic or microgeographic isolation and different soil preferences, sometimes but not always associated with shifts in pollination systems. Edaphic shifts appear to be the primary

Table 3.—Distribution of differences (indicated by an asterisk, *) among taxa of terminal sister groups of *Sparaxis* (inferred differences in parentheses). 1 = *S. caryophyllacea*-*S. tricolor* group; 2 = *S. tricolor*-*S. pillansii*; 3 = *S. calcicola*-*S. grandiflora* plus *S. bulbifera*; 4 = *S. grandiflora*-*S. bulbifera*; 5 = *S. fragrans*-*S. maculosa*; 6 = *S. auriculata*-*S. roxburghii*; 7 = *S. villosa*-*S. variegata* plus *S. metelerkampiae*; 8 = *S. variegata*-*S. metelerkampiae*

	1	2	3	4	5	6	7	8
Allopatry	*	-	-	-	*	*	-	-
Parapatry	-	*	*	*	-	-	*	*
Soil type	-	*	*	*	-	-	-	-
Pollinator	*	-	*	-	(*)	*	*	-

determinant of speciation for three species or species groups and geographical isolation for three more, both usually associated with pollinator shifts except for *Sparaxis grandiflora*-*S. bulbifera*. For *S. metelerkampiae* and *S. variegata* we see the primary ecological difference as a shift to a drier habitat and a change in reproductive compatibility. Geography alone is the evident driver in the differentiation of subspecies in *S. grandiflora*, but soil moisture and chemistry seem to have been important for differentiation in the *S. tricolor* clade, with a secondary pollinator shift. Deeper in the phylogeny, the species pair *S. bulbifera* and *S. grandiflora* represents a shift from large-bodied bee pollination to a generalist system, associated with loss of bilateral floral symmetry.



Taxonomic history

The taxonomic history of *Sparaxis* is remarkably complex for so small a genus. The first species known to science, *S. bulbifera*, was assigned by Linnaeus (1756) to *Ixia*, as were all southern African Iridaceae with spicate inflorescences and radially symmetric flowers. The three other species with radially symmetric flowers known at this time, *S. fragrans*, *S. grandiflora* and *S. tricolor* were likewise first placed in *Ixia*. The first known species of *Sparaxis* with zygomorphic flowers, *S. villosa* and its synonym *S. bicolor*, were at first referred to *Gladiolus* as was consistent with generic circumscriptions of the family in the 18th century.

The English botanist and specialist in geophytic plants, John Gawler (later John Bellenden Ker and for convenience now known to botany as Ker Gawler), made the first serious attempt to produce a more natural classification of the Ixioid Iridaceae, establishing the new genera *Anomatheca* (now *Freesia*), *Babiana*, *Geissorhiza*, *Hesperantha*, *Tritonia* and *Sparaxis* for species until then included in the three 18th century genera *Antholyza*, *Gladiolus*, and *Ixia* (Ker Gawler 1802, 1804a). Ker Gawler's circumscription of *Sparaxis* corresponds exactly to our current one—he included species with both radially symmetric and zygomorphic flowers in the genus. Thus, in 1804, *Sparaxis* included *S. villosa* (under its later synonym *S. bicolor*), *S. bulbifera*, *S. fragrans*, *S. galeata*, and *S. grandiflora*. The features uniting the genus included the dry, crinkled, often prominently cuspidate and somewhat lacerated floral bracts, and generally similar, slightly fleshy leaves, sturdy flowering stem and globose corms with pale, usually finely fibrous tunics.

This taxonomy survived for just 22 years, for in 1826 Robert Sweet described the new genus *Synnotia* (initially misspelled *Synnetia*) with the single species, *S. variegata*. The genus was named in honour of Walter Synnot, the landdrost (magistrate) at Clanwilliam from 1821 to 1825. Synnot, who collected plants in the Clanwilliam district and nearby (Gunn & Codd 1981), sent seeds and/or corms to Great Britain, among them *S. variegata*. The large, zygomorphic flower with its long perianth tube provided Sweet with the justification for his new genus. Later that year, Sweet added the zygomorphic-flowered *Sparaxis galeata* and *S. villosa* to *Synnotia*. *Sparaxis* and *Synnotia* remained separate genera in accounts of the Iridaceae by Klatt (1882) and Baker (1892, 1896). G.J. Lewis (1954), likewise, maintained *Synnotia* and Goldblatt (1969; 1971) also regarded the two as separate genera.

A third genus *Streptanthera*, now also included in *Sparaxis*, was described in 1827 by Sweet to include white-flowered *S. elegans* (Sweet 1827) and later the salmon-pink-flowered *S. cuprea* (Sweet 1831), for plants with a *Sparaxis*-like habit and floral bracts but remarkable coiled anthers of a chocolate-brown colour. *Streptanthera* was upheld by both Klatt (1882) and Baker (1892, 1896); Klatt also transferring *S. tricolor* here because of the nearly identical floral bracts that differed from those of other *Sparaxis* species then known. *Streptanthera* was united with *Sparaxis* by Goldblatt (1969) who noted that *Sparaxis pillansii*, which is closely related to *S. tricolor* and has identical floral bracts, had slightly sigmoid anthers (from a study site northeast of Nieuwoudtville), a feature rendering the twisted anthers of *S. elegans* of less significance. The initial two species of *Streptanthera* (*S. cuprea* and *S. elegans*) are now treated as colour morphs of a single species, *Sparaxis elegans*.

Synnotia was reunited with *Sparaxis* by Goldblatt (1991, 1992), who treated it as sect. *Synnotia*. The union of *Synnotia* with *Sparaxis* receives unambiguous support from molecular based phylogenetic analysis.

Systematics

Sparaxis *Ker Gawl.* in Sims, Curtis's Botanical Magazine 15: sub. t. 548 (Jan. 1802) et Ker Gawl. in Annals of Botany (König & Sims) 1: 225 (1804a). Type species: *S. bulbifera* (L.) Ker Gawl.

Synnotia Sweet: t. 150. 1826a (as *Synnetia*), corr. *Synnotia* by Sweet: 501 (1826b). *Sparaxis* sect. *Synnotia* (Sweet) Goldblatt: 57 (1991). Type: *S. variegata* Sweet (= *Sparaxis variegata* (Sweet) Goldblatt).

Streptanthera Sweet: t. 209 (1827). Type: *S. elegans* Sweet (= *Sparaxis elegans* (Sweet) Goldblatt).

Anactorion Raf: 34 (1838 as 1836). Type: *A. bicolor* (Thunb.) Raf. (= *Sparaxis villosa* (Burm.f.) Goldblatt).

Deciduous geophytes. *Corm* globose to conical, rooting from base; corm tunics of fine to moderately fine netted fibres or of coarse hard fibres often thickened below into claw-like ridges. *Stem* firm and relatively thick, ± erect, smooth, simple or branched, then either from near base or well above ground, sometimes with few, moderate sized axillary cormlets below, or many small cormlets in all axils. *Leaves* several, mostly basal, sometimes also cauline, lowermost 2 or 3 membranous and sheathing (thus cataphylls), foliage leaves green, with blades lanceolate to linear or falcate, obtuse to acute, often obliquely acuminate, smooth, often with many closely set fine secondary veins, with prominent central vein, margins sometimes thickened. *Inflorescence* a spike, (1–)few to several flowered, lax, 2-ranked in bud, loosely spiral or nearly secund in bloom; bracts dry and crinkled, pale-translucent with brown streaks, ± entire to lightly lacerate, or outer (abaxial) with 3 long tapering cusps, inner (adaxial) smaller than outer, with 2 long tapering cusps. *Flowers* actinomorphic or zygomorphic, then with either only stamens and style asymmetrically arranged or perianth also asymmetric and ± bilabiate with upper (adaxial) tepal larger and often hooded and lower three tepals smaller, with contrasting markings and ± horizontal or directed downward; perianth tube short to long, funnel-shaped (cylindric below and expanded above), sometimes obliquely so, or elongate, much exceeding bracts and dimorphic with lower part cylindric and abruptly bent and widened above; tepals subequal in radially symmetric flowers or, in zygomorphic flowers, dorsal largest; lanceolate to obovate or spathulate, acute to obtuse. *Stamens* inserted at base of expanded part (throat) of tube, symmetrically or asymmetrically disposed; filaments filiform, straight and surrounding style, or curved outwards with abaxial stamen twisted to lie opposite adaxial tepal, or all three filaments ± parallel and opposite adaxial tepal; anthers straight, curved or spirally coiled, sub-basifixed, extrorse or functionally introrse. *Ovary* ovoid; style filiform, straight and erect or unilateral, style branches either short, often with expanded tips, or long and filiform. *Capsules* barrel-shaped to ± globose, firm-membranous, showing outline of seeds. *Seeds* globose, relatively large, smooth, usually glossy, (2–)4–15 per locule. *Basic chromosome number* $x = 10$.

Species 16: native to South Africa and restricted to the winter rainfall zone in the southwestern corner of the country; centred in the southwestern Western Cape but extending north to the western Karoo and the southern margin of Namaqualand.

Key to species

1a Perianth zygomorphic, with adaxial (upper) tepal largest, erect and often hooded and lower three tepals usually smaller and ± horizontal; stamens unilateral and arcuate with anthers parallel and ± contiguous:

2a Narrow lower part of perianth > 25 mm long, well exserted from bracts; tube bent abruptly (geniculate) at top of slender part into wide throat:

3a Flowers with upper tepal 25–30 mm long; anthers 5–7 mm long; style reaching at least to apex and sometimes exceeding anthers; style branches 4–7 mm long and spreading beyond anthers . . . . 15. *S. variegata*

3b Flowers with upper tepal 14–17 mm long; anthers 3–4 mm long; style not reaching anther apices; style branches 2–3 mm long and tangled in anthers . . . . 16. *S. metelerkampiae*

2b Narrow part of perianth tube < 25 mm long, exserted or included in bracts; tube gently to sharply curved at top of narrow part:

4a Corm tunics of fine fibres; flowers smaller, dorsal tepal < 10 mm long; filaments 4.5–8 mm long:

5a Flowers 32–36 mm long from base of perianth tube to tip of dorsal tepal . . . . 4. *S. calcicola*

5b Flowers ± 18 mm long from base of perianth tube to tip of dorsal tepal . . . . 5. *S. parviflora*

4b Corm tunics either of fine or coarse fibres thickened into claws below; flowers usually larger, dorsal tepal at least 15 mm long; filaments 10–20 mm long:

6a Corm tunics of hard, claw-like fibres not extending upwards in a neck; upper tepal directed forwards and somewhat hooded over stamens; filaments 12–13 mm long:

7a Upper tepal ± 16 mm long; throat ± unmarked; base of leaves unmarked; style dividing opposite lower half of anthers, branches ± 2 mm long . . . . 14. *S. villosa*

7b Upper tepal 22–24 mm long; throat boldly marked with dark stripes; base of leaves lightly speckled with purple (not visible in dry material); style dividing near anther apices, branches ± 5 mm long . . . . 13. *S. caryophyllacea*

6b Corm tunics of fine fibres, usually extending upwards in a neck; upper tepal erect or directed backwards; filaments 15–20 mm long:

8a Cylindrical lower part of perianth tube < 8 mm long; leaf bases spotted red to purple (sometimes fading when dry) . . . . 12. *S. galeata*

8b Cylindrical lower part of perianth tube 15–25 mm long:

9a Leaf bases speckled, blades with prominent submarginal vein; perianth tube ± 18 mm long . . . . 10. *S. auriculata*

9b Leaf bases unmarked, blades without prominent submarginal vein; perianth tube 20–25 mm long . . . . 11. *S. roxburghii*

1b Perianth radially symmetric; stamens either symmetrically disposed around central style or abaxial stamen lying opposite adaxial tepal, and style eccentric and inclined opposite adaxial tepal:

10a Bracts 18–30 mm long, entire to slightly lacerate, always without discrete cusps; stamens symmetrically disposed around erect style; style branches 2–3 mm long:

11a Anthers spirally coiled and reaching only to apex of style; style branches greatly expanded . . . . 3. *S. elegans*

11b Anthers straight or slightly twisted and curved, extending well beyond style branches; style branches not greatly expanded:

12a Anthers straight, yellow to ochre; spikes 2–5 flowered; tepals orange marked with yellow and black . . . . 1. *S. tricolor*

12b Anthers incurved, slightly twisted, red to brown; spikes (2–)5–10 flowered; tepals rose pink, marked with yellow and red to purple . . . . 2. *S. pillansii*

10b Bracts 10–20 mm long, deeply lacerate with discrete cusps ± as long as or longer than rest of bract; stamens symmetrical or asymmetrical; style branches > 4 mm long:

13a Lateral margins of outer bracts irregularly serrate (or ± fringed); stamens symmetrically arranged around style; style branches ± 5 mm long:

14a Tepals with large black markings at base, 27–35 × 8–10 mm; leaves oblong to lanceolate, 9–12 mm wide and obliquely apiculate . . . . 9. *S. maculosa*

14b.Tepals unmarked, 18–25 × 5–8 mm; leaves linear to narrowly lanceolate, 2–5(–9) mm wide and acute . . . . 8. *S. fragrans*

13b Lateral margins of outer bracts ± entire, not serrate or fringed; stamens and style unilateral, thus asymmetrically disposed; style branches 6–10 mm long:

15a Stem usually branched in middle of stem and bearing one or more cauline leaves; many small cormlets produced after flowering at all nodes . . . . 7. *S. bulbifera*

15b Branches if present produced from base and stem lacking a cauline leaf; cormlets never produced above ground . . . . 6. *S. grandiflora*

I. Sect. **Streptanthera** *(Sweet) Goldblatt & J.C.Manning*, new combination and rank. *Streptanthera* Sweet: t. 209 (1827). Type: *Streptanthera elegans* Sweet (= *Sparaxis elegans* (Sweet) Goldblatt).

Plants with corm tunics of fine fibres. *Spike* with floral bracts without cusps, the outer deltoid and acute, becoming lacerate with age. *Flowers* radially symmetric, tepals variously coloured, predominantly orange, red, salmon or white; perianth tube short, funnel-shaped, up to 12 mm long. *Stamens* symmetrically arranged around central style, anthers straight or S-shaped, then coiled around style.

1. **Sparaxis tricolor** *(Schneev.) Ker Gawl.* in Annals of Botany (König & Sims) 1: 225 (1804a). Baker: 117 (1896). Goldblatt: 230 (1969). *Ixia tricolor* Schneev.: t. 39 (1794). *Streptanthera tricolor* (Schneev.) Klatt: 390 (1882). Type: South Africa, without precise locality or collector, illustration in Schneev.: t. 39 (1794).

Ixia tricolor Curtis: t. 381 (1797), illegitimate homonym, not *I. tricolor* Schneev. (1794). Type: South Africa, without precise locality or collector, illustration in Curtis: t. 381 (1797).

Sparaxis blanda Sweet: 398 (1826b). *S. tricolor* var. *blanda* (Sweet) Baker 16: 99 (1877). Type: South Africa, without locality or collector, illustration in Curtis's botanical magazine 36: t. 1482, δ, *floris subroseo-albida* (1812).

Sparaxis griffinii Sweet: 398 (1826b). *S. tricolor* var. *griffinii* (Sweet) Baker: 99 (1877). Type: South Africa, without locality or collector, illustration in Curtis's botanical magazine 36: t. 1482, γ, *floris violaceo-purpurea* (1812).

Sparaxis versicolor Sweet: t. 160 (1826c). *S. tricolor* var. *versicolor* (Sweet) Baker: 99 (1877). Type: South Africa, without precise locality or collector, illustration in Sweet: t. 160 (1826c).

Sparaxis lineata Sweet: t. 131 (1832). *S. grandiflora* var. *lineata* (Sweet) Baker: 99 (1877). *Streptanthera lineata* (Sweet) Klatt: 390 (1882). Type: South Africa, without precise locality or collector, illustration in Sweet: t. 131 (1832).

Plants mostly 300–400 mm high, with 1–3(–5) branches from base. *Corms* 10–20 mm diam., tunics of fine, pale, netted fibres. *Leaves* 5–10 in a basal fan, narrowly sword-shaped, acuminate, reaching ± to base of spike, 10–20 mm wide, closely veined with prominent main vein. *Spike* suberect, ± straight, 2–5-flowered, initially 2-ranked but ultimately subsecund; bracts dry, crinkled, light translucent brown with darker streaks, without visible veins, outer 20–30 mm long, narrowly deltoid, entire, later upper margins lacerate, inner usually slightly shorter, forked apically. *Flowers* radially symmetric, bright orange-scarlet, yellow in centre broadly edged with dark red-brown, unscented; perianth tube funnel-shaped, 9–12 mm long, lower narrow part ± 4.5 mm; tepals subequal, broadly lanceolate-ovate, 25–35 mm, outer 15–20 mm wide, inner 13–16 wide. *Stamens* symmetrically arranged, filaments 6–7 mm long, closely surrounding style, yellow, anthers linear, 8–9 mm long, weakly diverging, pale yellow, pollen white. *Style* dividing opposite lower third of anthers, branches 2–3 mm long, expanded in distal third, notched at apex. *Capsules* ± barrel-shaped, 6–7 mm long, showing outline of seeds. *Seeds* globose, glossy reddish brown, ± 2.0–2.5 mm diam., 4–8 per locule. *Chromosome number* 2*n* = 20. *Flowering time*: September, rarely in late August. Figure 2, Plate 1A.

Illustrations: Manning & Goldblatt: 83 (1997); Manning *et al*.: 2 & 360 (2002).

Distribution and biology: restricted to the northern end of the Bokkeveld Escarpment in Northern Cape, *Sparaxis tricolor* is known from just a few farms northwest and south of Nieuwoudtville (Figure 3). Plants grow in seasonally wet sites in loamy sand or among rocks along seasonal watercourses. The contrasting markings on the bright orange flowers with dark brown edged yellow in the centre of *S. tricolor*, also called the harlequin flower, represent beetle marks that attract pollinating insects, including the dark brown hopliine beetle, *Anisochelus inornatus* (Goldblatt *et al*. 2000). A second insect, the horsefly *Philoliche atricornis*, also visits the flowers and like the related *S. elegans*, *S. tricolor* may have a bimodal pollination system using both beetles and short-proboscid horseflies.

The species is naturalized in parts of Australia.

Conservation status: VU (Vulnerable), but we suggest EN (Endangered) is more appropriate in light of its narrow range and few popula-

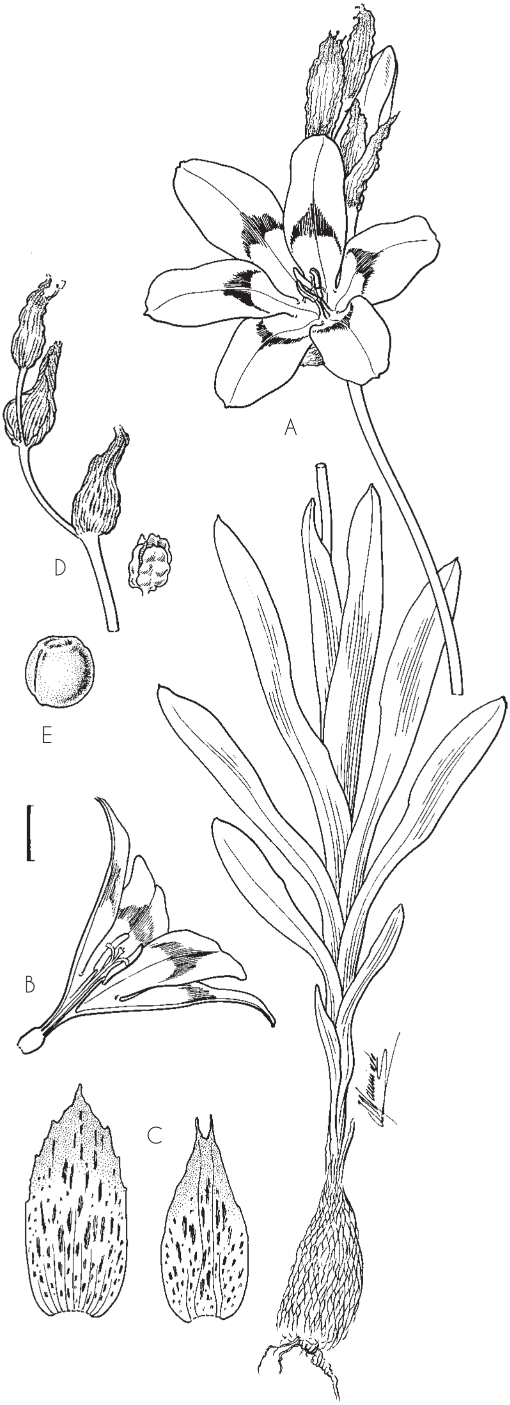


FIGURE 2.—*Sparaxis tricolor, Goldblatt & Manning 9463*. A, flowering plant; B, half-flower; C, outer (left) and inner (right) bracts; D, infructescence and detached capsule; E, seed. Scale bar: A, B, D, 10 mm; C, 5 mm; E, 2 mm. Artist: J.C. Manning.

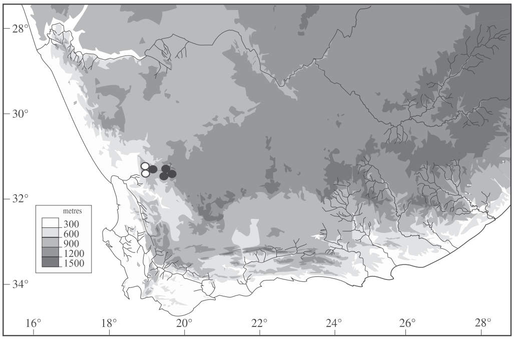


FIGURE 3.—Distribution of *Sparaxis tricolor*, ○; *S. pillansii*, ●.

tions; all threatened by farming activity and the unchecked spread of alien weeds.

Diagnosis and relationships: *Sparaxis tricolor* is recognized but its ± cup-shaped, radially symmetric, brilliant orange flowers with yellow centres edged in dark red-brown to almost black. The dark markings enclosing the yellow extend as a narrow line almost to the base of the tepals. The yellow stamens are erect and surround the style, which divides opposite the lower third of the anthers into short branches, 2–3 mm long.

The ± narrowly deltoid-ovate bracts of *Sparaxis tricolor* and allied *S. elegans* and *S. pillansii* differ from those of other species in the genus in lacking obvious veins, and the outer are initially entire and acute, later becoming irregularly torn. The bracts, also crinkled and flecked with dark brown streaks, are quite different to the cuspidate and sometimes long-cuspidate bracts of other species of the genus. In the related genera *Ixia* and *Tritonia*, the bracts usually have prominent veins on a pale translucent background and usually three short teeth at the vein tips. The radially symmetric flower is also derived in *Sparaxis*, contrary to past interpretations (e.g. Lewis 1954; Goldblatt 1969, 1992) that regarded radial symmetry as primitive and ancestral to the zygomorphic flower. Radial symmetry in *Sparaxis* is now believed to be a consequence of adaptation to hopliine beetle pollination (Goldblatt *et al*. 1998, 2000).

History: *Ixia tricolor* was described by the Dutch gardener George Voorhelm Schneevogt based on plants cultivated at Haarlem, The Netherlands. The well-executed painting by Schneevogt accompanying the description in his *Icones plantarum rariorum* (1794) leaves no doubt about the identity of the plant, but there is, unfortunately, no record of their source. The long history of plant collecting at the Cape (Goldblatt & Manning 2001) and their subsequent cultivation, first in Holland and later all over western Europe, make the early appearance of *Sparaxis tricolor* no surprise. Schneevogt's *Icones* appeared in multiple parts, each with three paintings, and *Ixia tricolor* (plate 39) was published in 1794 (Stafleu & Cowan 1985). All 48 plates were bound in a single volume and published in 1795. Plants cultivated in England some years later were described independently by Curtis (1797), who remarked that 'though new to this country, this plant has been known for some years to the Dutch; we find it in their catalogues under the name of *Ixia stellata tricolor*'. Minor colour variants, or possibly hybrids with other *Sparaxis* species, were named by Robert Sweet in the years 1826 to 1832, evidence of the favour that *S. tricolor* found in horticulture.

Ker Gawler included *Ixia tricolor* in his new genus *Sparaxis* when that genus was first described in 1802, and it has remained in the genus since then, except when Klatt (1882) transferred it to *Streptanthera*. Klatt's action received no support and Baker (1892, 1896) followed Ker Gawler's example in recognizing *Sparaxis tricolor.*

Sparaxis tricolor is widely cultivated in southern Africa and elsewhere today, and most *Sparaxis* hybrids were derived from crosses that included *S. tricolor*. Among the earliest of these were documented by Arabella Roupell (1849): a lovely bouquet in her *Specimens of the flora of South Africa* depicts both *S. elegans* and *S. tricolor* as well as a range of hybrids that appear to be crosses between *S. tricolor* and both purple- and white-flowered *S. grandiflora* (or possibly *S. bulbifera*). The painting, which depicts 15 different flower types in all, was executed during Roupell's visit to the Cape in 1843–44. Several species, including *S. bulbifera*, *S. tricolor*, *S. galeata* and some of the subspecies of *S. grandiflora*, were grown in Baron Ludwig's garden in Cape Town in the 1830s according to Ecklon (1827) and the hybrids painted by Roupell very likely came from this source.

Selection of hybrids and variants of *Sparaxis tricolor* continues today (Horn & Bundies 1989), and the species is grown for the container and specialist cut flower market in Europe. Plants with larger, longer-lasting flowers on taller stems have been bred, and several strains are polyploid (wild populations are diploid). It remains to be seen whether *Sparaxis* will make a significant impression in the horticultural trade, as have *Freesia* and *Gladiolus*, the two genera of southern African Iridaceae now firm favourites in the florist and nursery trade.

Representative specimens

NORTHERN CAPE.—**3119** (Calvinia): Farm Matjiesfontein S of Nieuwoudtville, (–AC), 16 Sept. 1992, *Goldblatt & Manning 9463* (MO, NBG); Nieuwoudtville, Grasberg, (–AC), 16 Sept. 1961, *Barker 9551* (NBG); Farm Biekoes, NW of Nieuwoudtville, (–AC), 5 Sept. 1985, *Snijman 910* (NBG).

2. **Sparaxis pillansii** *L.Bolus* in South African Gardening and Country Life 22: 57 (1932). Goldblatt: 232 (1969). Type: [Northern Cape], near Nieuwoudtville, Sept. 1931, *L. Bolus s.n.* (*BOL19182*, holo.!).

Plants 250–650 mm high, unbranched or with 1–3 branches from base. *Corm* 10–25 mm diam., tunics of moderately fine, netted fibres, often with fairly large cormlets in leaf axils. *Leaves* 8–10, all basal, reaching to ± middle of stem, lightly veined with central vein prominent. *Spike* sub-erect, lax, 4–9-flowered; bracts dry, translucent with dark brown streaks, outer narrowly deltoid, with single main vein, sometimes torn distally, 24–29 mm long, inner shorter to ± as long, often forked apically for up to 6 mm. *Flowers* radially symmetric, old rose fading to dull pink, tepals each with a heart-shaped yellow base edged in dark red to purple-brown, yellow in tube, unscented; perianth tube funnel-shaped, 7–9 mm long, lower slender portion ± 3 mm long; tepals subequal, lanceolate, subacute, 22–29 × 12–14 mm, remaining slightly cupped even when fully open. *Stamens* symmetrically arranged, filaments erect, ± 7.5 mm long, white, clasping style, anthers straight or slightly twisted in upper half, 7–8 mm long, red-purple or white with red-purple on adaxial surface. *Style* slender, white or red distally, dividing opposite middle of anthers, branches 2–3 mm long, slender, often slightly wider and bilobed distally, dark red, extending between anthers. *Capsules* ± barrel-shaped, ± 7 mm long. *Seeds* globose, glossy reddish brown, ± 2.5 mm diam., 4–6 per locule. *Chromosome number* unknown. *Flowering time*: late September to mid-October. Figure 4, Plate 1B.

Illustrations: Manning & Goldblatt: 10 & 81 (1997); Manning *et al*.: 360 (2002).

Distribution and biology: endemic to the Calvinia District in Northern Cape, *Sparaxis pillansii* is best known in the dolerite hills east of Nieuwoudtville but also occurs elsewhere on the Bokkeveld plateau, notably along streams on the slopes of the Hantamsberg at Calvinia, to the southwest on the Farm Driefontein, and on the heights of the Keiskie Mountains southeast of Calvinia (Figure 3). Plants are usually found growing in heavy red clay waterlogged for much of the growing season, sometimes in pools of standing water among dolerite boulders, but also in broken shale along seasonal washes and watercourses. Pollination biology is the same as in the closely related *S. elegans* and *S. tricolor*, the flowers being visited by hopliine beetles (*Clania glenlyonensis* in the Nieuwoudtville area but other species elsewhere) and also by the short-proboscid horse fly, *Philoliche atricornis*. Small empidid flies are also sometimes seen in the flowers and no doubt are able to accomplish cross pollination as they bear visible loads of the whitish pollen on their bodies.

Conservation status: R (Rare) or LC (Least Concern). The discovery of new populations south of Calvinia has significantly expanded the known range.

Diagnosis and relationships: the virtually identical form of the flowers strongly suggests that *Sparaxis pillansii* is closely related to *S. tricolor*, and this is borne out by the molecular phylogenetic analysis (Figure 1b), which shows *S. pillansii* and *S. tricolor* to be immediately related and sister to *S. elegans*. Only the old rose pigmentation with smaller central patterning, the red-purple anthers, and the more numerous flowers differentiate the two species. In some populations the anthers are very slightly twisted, a feature otherwise unknown in the genus, ex-

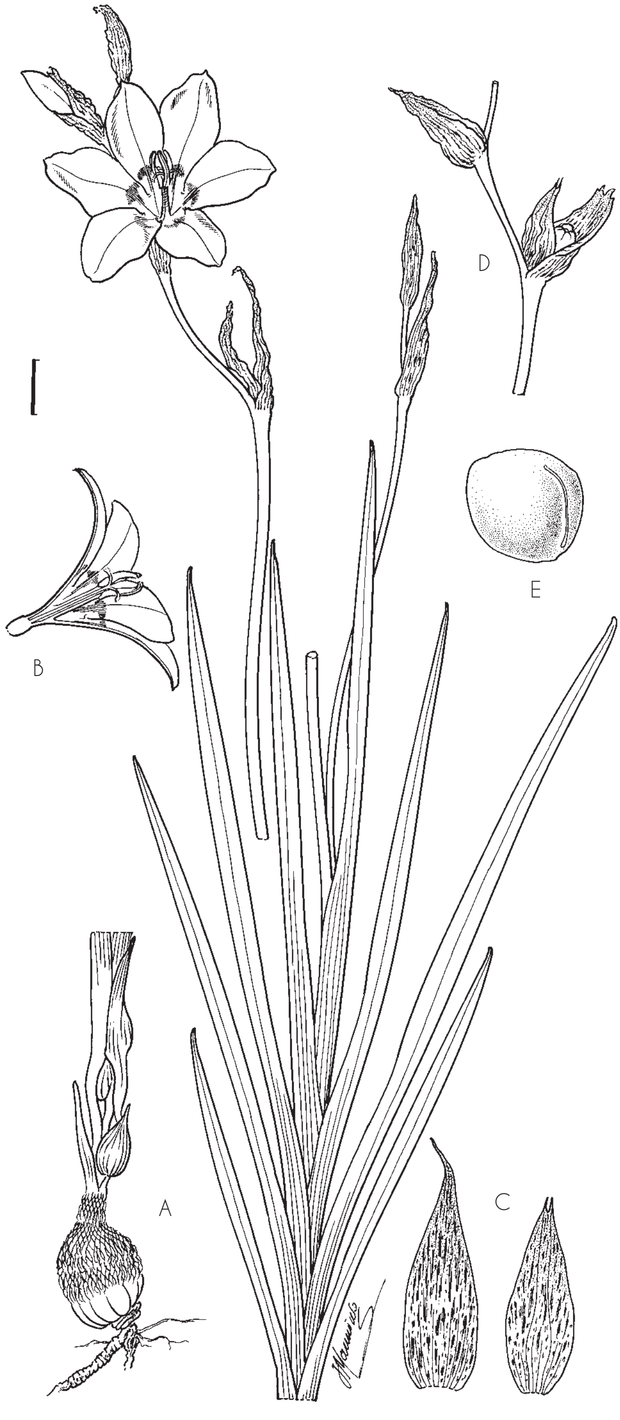


FIGURE 4.—*Sparaxis pillansii, Goldblatt, Manning & Porter 13369*. A, flowering plant; B, half-flower; C, outer (left) and inner (right) bracts; D, infructescence; E, seed. Scale bar: A, B, D, 10 mm; C, 5 mm; E, 3 mm. Artist: J.C. Manning.

cept for the exaggerated twisting of the anthers of *S. elegans*. *Sparaxis pillansii* is also typically a taller species, sometimes reaching 650 mm whereas *S. tricolor* seldom exceeds 350 mm. Ecologically, the two species occupy very different soil types.

History: it is surprising that *Sparaxis pillansii* remained unknown until the early 20th century, and we suspect that earlier records exist, although we have not seen any collected before 1916 when Rudolf Marloth documented its occurrence at Tulbagh, where it was evidently cultivated or naturalized. Marloth's collections from the dolerite hills east of Nieuwoudtville (1918) and at Driefontein Farm, southwest of Calvinia (1921), represent the first wild records. The collection from Driefontein was, incidentally, made at the same time and place as *S. galeata*, another species not until then recorded in the wild but well known from plants cultivated in Europe. Several other plants from the Bokkeveld Plateau were grown in Europe in the later 18th and early 19th centuries including closely allied *S. elegans* and *S. tricolor*, which indicates a modest level of botanical activity there long before *S. pillansii* was described. Soon after Marloth found the species, it was recollected by H.M.L. Bolus and her students in the late 1920s and early 1930s during their systematic exploration of the botany of the area around Nieuwoudtville. Bolus described *S. pillansii* in 1931 based on her own collection. Significantly, Bolus commented in her account of *S. pillansii* that it had been in cultivation at Kirstenbosch Gardens for some 10 years by then and was also grown in private gardens in Cape Town. She in fact first saw the species in the garden of botanist, Neville Pillans, in Rosebank 'nearly twenty years ago', which would have been about 1912. Bolus also mentions that hybrids between *S. pillansii* and *S. tricolor* frequently occur when the two are grown together as they did at Kirstenbosch in the 1920s. The *Sparaxis* hybrids available in the horticultural trade clearly have *S. pillansii* as well as *S. tricolor* in their ancestry, but the production of these hybrids has never been documented.

Representative specimens

NORTHERN CAPE.—**3119** (Calvinia): Bokkeveld, E of Nieuwoudtville, on dolerite hill (Rooikoppies), (–AC), Aug. 1918, ex hort. Marloth, *Marloth 7944* (PRE); Klip Koppies, Nieuwoudtville, (–AC), 15 Sept. 1961, *Barker 9530* (NBG); Glenlyon, Camel Koppie, (–AC), 17 Oct. 2001, *Nanni 176* (NBG); SE slopes at foot of the Hantamsberg near stream, (–BA), 16 Sept. 1980, *Goldblatt 5806* (MO, NBG); Farm Kareeboomfontein, (–DA), 3 Sept. 1974, *Hanekom 2378* (MO, PRE); Farm Driefontein, SW of Calvinia, 1 000 m, (–DA), Sept. 1921, *Marloth 10428* (PRE), 17 Sept. 2009, *Goldblatt, Manning & Porter 13376* (MO, NBG); Keiskie Mountains, S of Farm Keiskie, (–DB), 17 Sept. 2009, *Goldblatt, Manning & Porter 13369* (MO, NBG).

Cultivated (or naturalized): WESTERN CAPE.—**3319** (Worcester): Tulbagh, (–AC), Oct. 1916, *Marloth 7937* (PRE).

3. **Sparaxis elegans** *(Sweet) Goldblatt* in Journal of South African Botany 35: 233 (1969). *Streptanthera elegans* Sweet: t. 209 (1827). Type: South Africa, without precise locality or collector, figure in Sweet: t. 209 (1827).

Streptanthera cuprea Sweet: t. 122 (1831) [Sweet: 501 (1830) nom. nud.]. Baker: 86 (1896). Pole-Evans: pl. 320 (1928). *Sparaxis cuprea* (Sweet) Klatt: 378 (1867). Type: South Africa, without precise locality or collector, figure in Sweet: t. 122 (1831).

Streptanthera cuprea var. *non-picta* L.Bolus: 276 (1932). Marais: t. 557 (1969). Type: [Northern Cape], Nieuwoudtville, *Buhr s.n.* (*BOL19443*, holo.!).

Illustrations: Marais: t. 557 (1969) [uniformly coloured morph]; Manning & Goldblatt: 83 (1997); Manning *et al*.: 357 (2002).

Plants 100–300 mm high, stem usually simple or branching from base. *Corm* 10–17 mm diam., tunics of moderately fine, pale fibres. *Leaves* 5–9, ± as long as stem, 5–14 mm wide, closely veined with midrib prominent. *Spike* flexed at base of first flower, mostly 3–5-flowered; bracts dry, crinkled, pale-translucent with brown streaks, without visible veins, outer 18–22 mm long, deltoid, entire or lacerate apically, inner 16–20 mm long, forked apically. *Flowers* radially symmetric, predominantly salmon-pink or white, purple in centre edged distally with a violet transverse band containing yellow transverse marks and a pale streak in centre of each tepal, unscented; perianth tube funnel-shaped, 6–10 mm long, narrow basal part 2–3 mm long; tepals subequal, ovate, spreading horizontally when fully open, 18–32 × 14–21 mm. *Stamens* symmetrically arranged, filaments 5–7 mm long, purple, anthers tightly S-shaped and twisted around style, ± 4 mm long, maroon, pollen red-brown. *Style* yellow below, purple distally, dividing opposite anther tips, branches ±

FIGURE 5.—*Sparaxis elegans*, *Goldblatt 4286*. A, flowering plant; B, half-flower; C, outer (left) and inner (right) bracts; D, stamens and style; E, detail of style branches; F, infructescence; G, seed. Scale bar: A, B, F, 10 mm; C, 5 mm; D, E, G, 2 mm. Artist: J.C. Manning.

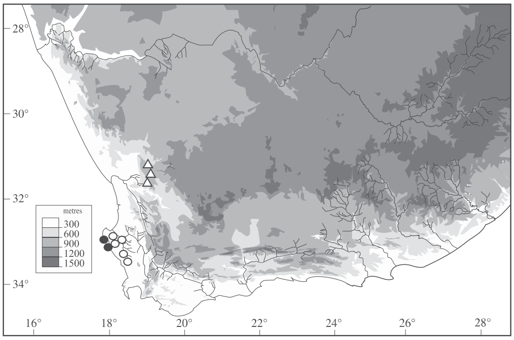


FIGURE 6.—Distribution of *Sparaxis elegans*, Δ; *S. calcicola*, ●; *S. parviflora*, ○.

2 mm long, strongly broadened distally and ± 2 wide, bilobed at tips. *Capsules* globose, mostly 6–8 mm long, enclosed by bracts. *Seeds* usually 6 per locule, globose, glossy dark reddish brown, ± 2 mm diam. *Chromosome number* 2*n* = 20. *Flowering time*: September. Figure 5, Plate 1C,D.

Distribution and biology: restricted to the western Bokkeveld Plateau and the Bokkeveld Mountains, *Sparaxis elegans* extends from a short distance north of Nieuwoudtville southward to the Klein Kobee; thus straddling the Northern Cape / Western Cape boundary (Figure 6). Plants grow on stony, tillite-derived soils in the north and on clays in the south but always in renosterveld. The strikingly coloured and patterned flowers are pollinated by hopliine beetles and the short-proboscid horsefly, *Philoliche atricornis*; the former using the flowers for sites of assembly and copulation, and the latter seeking the minute traces of nectar that the flowers produce. To date all pollination observations have been made on salmon-flowered northern populations.

Conservation status: VU (Vulnerable).

Diagnosis and relationships: *Sparaxis elegans* is easily recognized by the distinctively marked flowers, purple anthers coiled around the style, red-brown pollen, and unusually broad style branches. The more common form with salmon-pink flowers occurs in the Nieuwoudtville area, with the white flowered form in the south of its range. The two colour morphs usually occur in pure stands, but we have seen white morphs mixed with the salmon at a few sites. The shift from salmon to white flowered populations is abrupt.

History: we have no record of the source of plants cultivated in Great Britain in the 1820s that were the basis for Robert Sweet's two *Streptanthera* species, *S. elegans* or *S. cuprea*. Sweet obtained plants (whether seeds or corms is not recorded) from Walter Synnot, Landdrost or Magistrate at Clanwilliam (see Taxonomic history, above), including what became the type of *Synnotia variegata* (now *Sparaxis variegata*), and we speculate that he might also have provided Sweet with his *Streptanthera* plants. The history of *Streptanthera* and its transfers into and back out of *Sparaxis* have been discussed above and it remains only to mention that it was not until 1969 that the salmon-flowered *S. cuprea* was regarded merely as a colour variant of *S. elegans* (Goldblatt 1969). We do not recognize *Streptanthera cuprea* var. *non-picta*, described by H.M.L. Bolus in 1931 and based on plants with uniformly coloured flowers—it is merely an occasional mutant or colour sport.

Representative specimens

NORTHERN CAPE.—**3119** (Calvinia): Klipkoppies, Nieuwoudtville, (–AC), 15 Sept. 1961, *Barker 9536* (NBG); Nieuwoudtville, N end of blommepad (trekpad), W of town (Farm Willemsrivier), (–AC), 26 Sept. 2002, *Nanni 340* (NBG); Nieuwoudtville Reserve, (–AC), 8 Sept. 1983, *Perry & Snijman 2343* (NBG); Nieuwoudtville, Glenlyon Farm, (–AC), 15 Sept. 1961, *Lewis 5909* (NBG); 5 km S of Nieuwoudtville, (–AC), 1 Oct. 1976, *Goldblatt 4286* (MO); Nieuwoudtville, Farm Groot Tuin, (–AC), 19 Sept. 2002, *Pretorius 796* (MO, NBG); Oorlogskloof Nature Reserve, 15 km SSW of Nieuwoudtville, Farm Driefontein, Kranskloof 792, (–CA), 7 Oct. 1996, *Pretorius 371* (NBG).

WESTERN CAPE.—**3119** (Calvinia): 1 km N of Klein Kobee, Langfontein, (–CA), 4 Sept. 2006, *Helme 4241* (NBG).

II. Sect. **Sparaxis**

Sparaxis sect. *Synnotia* (Sweet) Goldblatt in Contributions from the Bolus Herbarium 13: 57 (1991). *Synnotia* Sweet: t. 150 (1826a, as *Synnetia*), corr. *Synnotia* by Sweet : 501 (1826b). Type: *Synnotia variegata* Sweet (= *Sparaxis variegata* (Sweet) Goldblatt subsp. *variegata*).

Plants with corm tunics of fine or coarse fibres. *Spike* with floral bracts with prominent cusps, these often brown. Flowers zygomorphic or radially symmetric, tepals yellow often marked with purple, white, or purple; perianth tube funnel-shaped, short or up to 20 mm long or elongate and ± cylindric. *Stamens* unilateral or symmetrically arranged around central style, anthers straight.

4. **Sparaxis calcicola** *Goldblatt & J.C.Manning*, sp. nov.

TYPE.—Western Cape, 3217 (Vredenburg): Jacobsbaai, crevices in limestone pavement, (–DD), 25 Aug. 2007, *Goldblatt*, *Manning & Porter 12894* (NBG, holo.; K, MO, PRE, S, iso.).

Plants mostly 120–220 mm high, stem usually unbranched or with 1(2) branches from base, occasionally also from middle of stem, without cormlets in lower leaf axils. *Corm* 8–14 mm diam., tunics of pale, fine fibres, often matted together. *Leaves* 5–8, obtuse to acute or obliquely apiculate, usually reaching to ± base of spike or sometimes shortly exceeding it, (3–)5–10 mm wide, with prominent main vein, occasionally with thickened margins. *Spike* 3–5-flowered, branches with fewer flowers, weakly flexuose, suberect; bracts dry, wrinkled, pale with dark brown streaks below, rust-brown above, outer 12–14 mm long, irregularly lacerate with 3 prominent cusps, inner 10–12 mm long, 2-cusped. *Flowers* bilabiate, upper tepals creamy white, upper lateral and lower tepals yellow with dark mark at limb base, lightly lemon-scented; perianth tube obliquely funnel-shaped, curving outwards above, 13–15 mm long; tepals unequal, dorsal largest, erect, 20–22 × 8–10 mm, widest in midline, upper laterals spreading at right angles to tube, 14–16 × ± 6 mm long, lower tepals united in lower 2–3 mm, narrowed at base of free part into claws ± 3 mm long, expanding abruptly into oblong limbs ± 10 mm × ± 5 mm, channeled in lower half, spreading horizontally. *Stamens* unilateral, filaments arched, ± 8 mm long, white, anthers parallel, ± 4 mm long, pollen creamy yellow. *Ovary* ± 3.5 mm long, ovoid-trigonous, style arching above filaments, white, dividing opposite anther tips, branches diverging to weakly recurved, ± 3 mm long, expanded apically and ciliate on margins, convolute below apex. *Capsules* barrel-shaped, (7–)9–11 mm long. *Seeds* 4–6 per locule, globose, yellowish brown, 2.2–2.5 mm diam.. *Chromosome number* unknown.

Flowering time: early August to mid-September. Figure 7, Plate 2A.

Distribution and biology: restricted to the rocky limestone hills and coast immediately north and west of Saldanha Bay, *Sparaxis calcicola* occurs in loamy soil in limestone pavement and in calcrete (Figure 6). Plants grow in low scrub dominated by *Osteospermum moniliferum* L. (Asteraceae) and among several other, mainly edaphic endemics of the Saldanha coast, including *Ferraria densepunctulata* M.P.de Vos, *Ixia purpureorosea* G.J.Lewis, *Romulea barkerae* M.P.de Vos (Iridaceae), *Felicia elongata* (Thunb.) O.Hoffm. and *Tripteris calcicola* J.C.Manning & Goldblatt (Asteraceae). The moderate-sized but brightly coloured and fragrant flowers are pollinated by *Apis mellifera* and possibly other large bees, which are rewarded by the small quantity of sweet nectar secreted in the base of the tube. The flowers are protandrous, but the stigmatic tips of the style branches recurve late in the flowering cycle and only then come in contact with pollen, and we infer the species is an obligate outcrosser. This awaits confirmation in the laboratory.

Conservation status: moderately common where it occurs, the range of *Sparaxis calcicola* is limited to a few kilometres of coastline, part of it already developed for housing. We propose a rating of VU (Vulnerable) for the new species, in light of the very narrow range and urban expansion in the vicinity of Saldanha.

Diagnosis and relationships: although first collected by Stellenbosch botanist, Charles Boucher, in 1993, this record was misidentified as *Sparaxis bulbifera*, and the species only came to our attention during a plant survey of Jacobsbaai, north of Saldanha, in 2006. *S. calcicola* is readily recognized by the bilabiate flower with a suberect dorsal tepal larger than the upper laterals, the short, arcuate stamens, and corms with tunics of fine, netted fibres. The flower is most like that of the more widespread *S. villosa*, which is, however, restricted to clay soils and has smaller flowers, the dorsal tepal somewhat hooded over the stamens, and corm tunics of coarse, claw-like fibres. The finely fibrous tunics and similarly oriented suberect dorsal tepal of *S. calcicola* recall *S. parviflora*, and the molecular phylogeny (Figure 1a, b) retrieves the two species as closely related,

FIGURE 7.—*Sparaxis calcicola*, *Goldblatt, Manning & Porter 12894*. A, flowering plant; B, flower, front view and half-flower; C, outer (left) and inner (right) bracts; D, infructescence; E, seed. Scale bar: A, B, D, 10 mm; C, 5 mm; E, 2 mm. Artist: J.C. Manning.

sharing a clade with *S. bulbifera* and *S. grandiflora*. *S. parviflora* has much smaller flowers, less than half the size of those of *S. calcicola*, the dorsal tepal ± 9 mm long and the tube 8–9 mm long.

Representative specimens

WESTERN CAPE.—**3217** (Vredenburg): Jacobsbaai, Swartriet Farm, calcrete ridge, (–DD), 7 Aug. 1993, *Boucher 5814* (NBG); hills N of Saldanha, among limestone rocks, (–DD), 13 Sept. 2008 (fr.), *Goldblatt & Porter 13119* (MO, NBG). **3318** (Cape Town): Langebaan Peninsula, Posberg, (–AB), Sept. 2011, *Goldblatt &Manning s.n.* (sight record only).

5. **Sparaxis parviflora** *(G.J.Lewis) Goldblatt* in Annals of the Missouri Botanical Garden 79: 155 (1992). *Synnotia parviflora* G.J.Lewis: 140 (1956). Type: South Africa, [Western Cape], between Darling and Mamre, Sept. 1953, *Lewis 3556* (SAM, holo.!; K!, iso.).

Plants 90–200 mm high, stem simple or branched from near base. *Corm* 10–15 mm in diam., tunics of fine, pale, ± matted fibres. *Leaves* 5–7, obliquely apiculate, basal except uppermost, this inserted shortly above ground level, 7–14 mm at widest, sheathing lower part of stem. *Spike* (1–)3–5-flowered, weakly flexuose, secund; bracts pale below with whitish veins, becoming irregularly flecked or streaked with brown distally, 10–15 mm long, outer obscurely 3–5-lobed, central lobe always longest, inner ± as long as outer, 2–4-lobed, but with 2 prominent, acute central lobes. *Flowers* bilabiate, upper three tepals mauve or creamy yellow and lower three tepals yellow with mauve or white tips, often with dark spots at base, abaxial half of throat darkly streaked, with weak spicy-sweet or rosy scent; perianth tube narrowly funnel-shaped, lower part clasping style, upper part curving outward, 8–9 mm long; tepals unequal, upper three largest, dorsal erect, 9–10 × ± 5 mm, upper laterals spreading at right angles to tube, ± 8.0 × 5.5 mm, lower three tepals united for ± 2 mm, lower laterals broadly channeled, horizontal with tips curving upward, ± 8.0 × 3.5 mm, lowermost held somewhat below lower laterals, 8 × 5 mm. *Stamens* unilateral, arcuate, filaments ± 4.5 mm long, reaching only to mouth of tube, white, anthers ± 4 mm long, purple when upper tepals mauve or white with violet lines on locule sutures, pollen ± white. *Ovary* 3–4 mm long, oblong-trigonous, style arched adaxial to filaments, white, dividing ± opposite anther bases, branches diverging, recurved distally, ± 3.5 mm long, channeled, ciliate along margins ± to base, slightly wider in upper half. *Capsules* barrel-shaped, 9–10 × ± 7 mm. *Seeds* (4)5 or 6 per locule, dark reddish brown, 2.4–2.8 mm in diam. *Chromosome number* 2*n* = 20. *Flowering time*: mid-August to mid-September. Figure 8, Plate 2B.

Illustrations: Manning & Goldblatt: 66 (1996); Manning *et al*.: 359 (2002).

Distribution and biology: restricted to the coastal plain between Mamre and Saldanha Bay, *Sparaxis parviflora* occurs in sandy ground or in gritty, granite derived soil, often in granite outcrops (Figure 6). Flowering occurs fairly early in the season and plants are usually in fruit by mid-September. *S. parviflora* is facultatively autogamous, not surprising in a plant with such small, inconspicuous flowers. In the wild the weakly scented flowers are often visited by honey bees attracted by the nectar.

Conservation status: NT (Near Threatened) but our field experience suggests VU (Vulnerable) as its range is much reduced, and some populations are severely impacted by development along the Atlantic coast of Western Cape.

Diagnosis and relationships: *Sparaxis parviflora* is immediately recognized by its tiny flowers, the smallest in the genus, with white or mauve upper tepals and yellow lower tepals with white or mauve tips, and the finely fibrous corm tunics. The small flowers have a dorsal tepal ± 10 mm long and the three lower, ± 8 mm. The plants are also fairly small and slender; the leaves seldom more than 12 mm wide, and the total height usually less than 15 mm and more often less than 10 mm. In contrast, the seeds are the largest in the genus, up to 2.8 mm in diameter. The flowers are usually white and yellow, sometimes with a slight purple flush on the outside, especially as they age. Plants from Langebaan have mauve upper tepals even in young flowers. In shape and colour the flowers are most like those of *S. calcicola*, but this species has much larger flowers, 20–22 mm long. Some forms of *S. villosa* have particularly small flowers, the upper tepal ± 10

FIGURE 8.—*Sparaxis parviflora*, *Goldblatt 2337*. A, flowering plant; B, half-flower; C, outer (left) and inner (right) bracts; D, infructescence; E, seed. Scale bar: A, B, D, 10 mm; C, 5 mm; E, 2 mm. Artist: J.C. Manning.

mm long, and confusion between them is best avoided by examination of the corms. Tunics of *S. villosa* are coarsely fibrous and ± clawed below, contrasting starkly with the finely fibrous tunics of *S. parviflora*. Based on chromosome counts for a single population, *S. parviflora* is tetraploid with 2*n* = 40, the only known polyploid in the genus in which the other 10 species counted are diploid.

History: The earliest records of *Sparaxis parviflora* date from the late nineteenth century when Rudolf Schlechter collected it near Hopefield, northwest of Cape Town, in September 1894 but it was treated as a form of *S. villosa* until recognized as a distinct species by G.J. Lewis in 1956 in her revision of *Synnotia*.

Representative Specimens

WESTERN CAPE.—**3318** (Cape Town): Langebaan (–AA), *Salter 3025* (BOL); Olifants Kop, Langebaan, granite outcrop, (–AA), 15 Sept. 1974, *Goldblatt 2337* (MO); Langebaan, Akkers farm, (–AA), 16 Aug. 1966, *Pamphlett 83* (NBG); between Langebaan and Waschklip, *Bachmann 2072* (Z); fields near Hopefield (–AB), 12 Sept. 1894, *Schlechter 5304* (BOL, C, E, MO, Z), Sept. 1905, *H. Bolus 12853* (BOL, K, MO); near Darling (–AD), Sept. 1944, *Lewis 1047* (SAM); Darling Reserve, (–AD), 11 Aug. 1960, *Lewis 5716* (NBG), 29, Aug., *Winkler 127* (BOL, NBG); Mamre Hills, (–AD), 22 Sept. 1942, *Barker 1802* (NBG), 23 Aug. 1947, 25 Aug., *Barker 4597* (NBG); between Darling and Mamre, (–AD), *Lewis 3556* (K, SAM).

6. **Sparaxis grandiflora** *(D.Delaroche) Ker Gawl.* in Annals of Botany (König & Sims) 1: 225 (1804a). Baker: 116 (1896). Goldblatt: 239 (1969). *Ixia grandiflora* D.Delaroche: 23 (1766). Type: South Africa, [Western Cape], near Tulbagh Road Station, 9 Sept. 1968, *Goldblatt 303* (BOL, neo.!, designated by Goldblatt: 239 (1969); MO!, iso.).

Plants mostly 120–300 mm high, stem simple or 1–3(–5)-branched from base. *Corm* globose, 6–15 mm diam., tunics of fine, pale netted fibres. *Leaves* 6–10, in basal fan, ± lanceolate to weakly falcate, mostly half to two thirds as long as stem, (4–)7–12 mm wide, obtuse-acuminate or acute, with prominent main vein and numerous fine secondary veins. *Spike* suberect or inclined, mostly 2–6-flowered; bracts dry, crinkled, pale, usually with brown streaks, 12–16(–20) mm long including cusps, outer ± lacerated distally, with 3 prominent, laxly twisted dark brown cusps, inner slightly smaller, with 2 prominent cusps. *Flowers* with radially symmetric perianth but unilateral stamens, white to pale or deep yellow with outer tepals often flushed purple on reverse and often with dark mark at base of tepals, or violet or dark plum-purple but pale in tube, usually unscented but sometimes faintly sweet scented or strongly scented of *Freesia*; perianth tube widely funnel-shaped, 10–14 mm long, narrow basal part 3–5 mm long; tepals subequal or outer 3 slightly larger, 22–45 × 10–18(–25) mm. *Stamens* unilateral but diverging, abaxial stamen twisted to lie against adaxial tepal, filaments 7–10 mm long, anthers facing center of flower, 7–12(–14) mm long, white. *Ovary* ovoid, ± 3 mm long, style unilateral, slender, white, lying against adaxial tepal, dividing opposite middle of anthers or up to 2 mm beyond anther tips, branches filiform, 6–9 mm long. *Capsules* ± barrel-shaped, 6–10 mm long, *Seeds* 7 or 8 per locule, ± 1.8 mm diam. *Diploid chromosome number* 2*n* = 20. *Flowering time*: August to September. Figure 9.

Distribution and biology: relatively widespread in the southwestern Cape but seldom common, *Sparaxis grandiflora* extends from Clanwilliam (and possibly Graafwater) in the northwest to Bredasdorp in the southeast (Figure 10). Plants occur at low elevations and usually favour heavy clay soils, but are occasionally found on sandy ground, often waterlogged in winter. We maintain the four subspecies recognized by Goldblatt (1969) and discuss their biology and conservation status individually.

Diagnosis and relationships: *Sparaxis grandiflora* is readily recognized by a combination of the unilateral orientation of the stamens in the otherwise radially symmetric perianth and the basal branching pattern. Unlike most species of Iridaceae with unilateral stamens, the filaments are not parallel with contiguous anthers but are divergent and held well apart from one another (Figure 9). Axillary branches on the stem, when present, are produced close to the base of the plant and always below ground level, and the main stem and branches bear short cauline leaves close to ground level at nodes hidden by the sheaths of the basal leaves. Only *S. bulbifera* has similarly unilateral stamens and a radially symmetric perianth, but this species always bears cauline leaves, and branches arise on the upper

FIGURE 9.—*Sparaxis grandiflora* subsp. *acutiloba*, *Goldblatt 2438*. A, flowering plant; B, half-flower; C, outer (left) and inner (right) bracts; D, infructescence; E, seed. Scale bar: A, B, D, 10 mm; C, 5 mm; E, 2 mm. Artist: J.C. Manning.

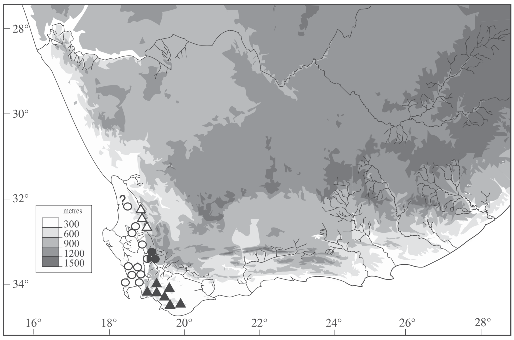


FIGURE 10.—Distribution of *Sparaxis grandiflora* subsp. *fimbriata*, ○; subsp. *grandiflora*, ●; subsp. *acutiloba*, Δ; subsp. *violacea* ▲.

part of the stem. After flowering in *S. bulbifera*, numerous small cormlets are produced at the aerial nodes in addition to larger cormlets at the underground nodes. The tepals are also consistently ovate in *S. bulbifera* but are often slightly spathulate in *S. grandiflora*.

Variation: *Sparaxis grandiflora* is unusually variable in flower colour and tepal shape and as a result Goldblatt (1969) recognized four allopatric subspecies that have since been maintained (Goldblatt 1999). Although finely drawn, each subspecies seems to represent a separate race of the species. The subspecies are geographically isolated from one another by mountain ranges and associated edaphic barriers. Bright yellow-flowered plants in the Olifants River Valley have relatively narrow tepals and represent subsp. *acutiloba*. Distributed west and southwest of the Olifants River Mountains, subsp. *fimbriata* has white to pale yellow flowers, often with dark markings at the bases of the tepals. We also tentatively include here a collection of purple flowered plants said to have been collected near Graafwater. The populations with pale yellow flowers in the hills north and west of the Piketberg have the broader tepals of subsp. *fimbriata* and are included in that subspecies but are obviously intermediate in perianth colour between typical subsp. *fimbriata* and yellow-flowered subsp. *acutiloba*.

In the Tulbagh Valley the typical form of *Sparaxis grandiflora*, mostly with intensely pigmented, plum-purple flowers and slightly spathulate tepals, is largely isolated from subsp. *fimbriata* by the Elandskloof Mountains. Plants from the Caledon district east of the Hottentots Holland Mountains and treated as subsp. *violacea* have pale violet or white flowers with markedly obtuse and often spathulate tepals. Populations that we have examined have flowers strongly scented of freesia, but flowers of other subspecies have at best only a faintly flowery scent or no scent at all.

History: *Sparaxis grandiflora* made its appearance in the scientific literature as *Ixia grandiflora*, applied by Daniel Delaroche in 1766 to the purple-flowered variant, now subsp. *grandiflora*. Delaroche also described *I. monanthos*, which is most likely what is now recognized as subsp. *acutiloba*. Both were evidently cultivated in Holland in the 1760s and perhaps earlier. In the following year, Linnaeus (1767) described *Ixia uniflora*, the type of which closely matches purple-flowered subsp. *grandiflora*. Evidently a popular and easily cultivated plant, subsp. *grandiflora* was independently described as *Ixia holosericea* by Jacquin (1797) and as *I. aristata* var. *atropurpurea* by Ker Gawler in Andrews (1800). We discuss in more detail the history of *S. grandiflora* under the individual subspecies.

Key to subspecies

1a Flowers dark plum-purple (rarely white mutants present); tepals spathulate; plants from Tulbagh Valley, rarely westwards to Gouda . . . . 6b. subsp. *grandiflora*
1b Flowers white, yellow or pale violet to light purple; tepals spathulate to narrowly ovate:
  2a Flowers clear, deep yellow; tepals narrowly ovate, acute or subacute; plants from Olifants River Valley . . . . 6c. subsp. *acutiloba*
  2b Flowers white, pale yellow, cream-coloured or pale violet; tepals ovate to spathulate, obtuse:
    3a Tepals spathulate, white, sometimes marked with violet or uniformly pale violet; usually strongly scented of freesia; plants from east of Hottentots Holland Mountains . . . . 6d. subsp. *violacea*
    3b Tepals narrowly ovate, usually white to pale yellow (?rarely purple), when white to pale yellow often mauve on reverse of tepals, not obviously scented; plants from west of Olifantsrivier-Hottentots Holland Mountain axis . . . . 6a. subsp. *fimbriata*

6a. subsp. **fimbriata** (*Lam.) Goldblatt* in Journal of South African Botany 35: 242 (1969). *Ixia fimbriata* Lam.: 339 (1789). *Sparaxis fimbriata* (Lam.) Ker Gawl.: 226 (1804a). Type: South Africa, without precise locality or collector, illustration in Miller: t. 237, fig. 1, 2 (1758).

Ixia sparsa Mill.: 7 (1768). Type: uncertain, possibly illustration in Miller: t. 237, f. 1 and f.2 (1758).

Ixia lacera L. ex Ker Gawl.: t. 548 (1802) et Roem. & Schult.: 398 (1817), pro syn. (based on *LINN58/18 & 58/19*).

Sparaxis lacera L. [as Herb. Banks] ex Ker Gawl.: 226 (1804a), pro syn.

Ixia liliago DC. in Redouté: t. 109 (1805). *Sparaxis grandiflora* var. *liliago* (DC.) Ker Gawl.: t. 258 (1818). *S. liliago* (DC.) Sweet: 398 (1826b). Type: South Africa, without precise locality or collector, illustration in Redouté: t. 109 (1805).

Sparaxis grandiflora var. *striata* Sweet: 501 (1830). Type: South Africa, without precise locality or collector, illustration in Curtis's Botanical Magazine 20: t. 779 (Oct. 1804b).

Plants up to 300 mm high. *Leaves* ± sword-shaped, lowermost sometimes falcate, obtuse- to acute-acuminate, two thirds to ± as long as stem. *Flowers* mostly white, cream or pale yellow (?rarely purple), yellow in throat, bases of tepals each with small to prominent dark-purple-black spot, flushed grey-mauve to purple on reverse of outer tepals; tepals obovate or elliptic, 28–40(–45) × (8–)10–16(–23) mm, obtuse or subacute. *Stamens*: anthers 9–10 mm long. *Style* dividing between middle and apex of anthers, branches (5–)7–9 mm long. Figure 9, Plate 2C.

Illustrations: Manning *et al*.: 358 (2002); Le Roux *et al*.: 52 (1981) [Piketberg morph].

Distribution: subsp. *fimbriata* extends from the Cape Peninsula and Somerset West in the south through the Boland and Swartland to the Piketberg in the north (Figure 10). We tentatively include here an unusual, outlying population with purple flowers said to have been collected from just north of Graafwater. Once common on the flats between Wellington and Gouda, increasing agricultural activity has restricted the subspecies to a few isolated populations across its once extensive range.

Conservation status: currently LC (Least Concern), but NT (Near Threatened) seems to us more appropriate in light of urban development and agricultural expansion virtually throughout its range.

Diagnosis: subsp. *fimbriata* is distinguished by the white to cream or pale yellow flowers with ovate tepals mostly 28–40 mm long. An unusual collection included here, *Van Breda 333* (PRE), and known only from a poorly localized site north of Graafwater has atypical purple flowers but appears otherwise to conform to subsp. *fimbriata*, although the tepals are unusually narrow, 8–9 mm wide. We have been unable to relocate this population. Phillip van Breda was curator of the Worcester Veld Reserve at the time, and it is possible that he mislabelled a collection of purple-flowered subsp. *grandiflora* from the Tulbagh Valley, but the tepals of the Graafwater plants are not markedly spathulate as they should have been if this was the case. Occasional purple flowered plants recorded at Voëlvlei, near Gouda, have the broad, spathulate tepals of subsp. *grandiflora* and are included in that subspecies. Particularly large flowered plants occur in the Darling area (e.g. *Goldblatt 6284*) with tepals up to 45 mm long and to 23 mm wide. Populations at low elevations east and west of the Piketberg Mountains have pale yellow flowers with the tepals sometimes acute at the tips and thus approach subsp. *acutiloba*.

History: the first record in the literature of subsp. *fimbriata* is the illustration in Philip Miller's (1758) *Figures of plants*, where on t. 237, f. 1 and f. 2 have illustrations of a white flowered *Sparaxis* (f. 3 of that plate has the purple flowered subsp. *grandiflora*), described by Miller in polynomial form. These two paintings are the type of *Ixia fimbriata* Lamarck (1789) and probably of *Ixia sparsa* Miller (1768), but the protologue of that species has no direct reference to either painting, nor does the formal description exactly match the polynomials. We provisionally cite *Ixia sparsa* in the synonymy of subsp. *fimbriata*. There are no other known possible types of *I. sparsa*. Ker Gawler recognized Lamarck's *I. fimbriata* as a species of *Sparaxis* in 1804, making the combination *S. fimbriata*, incidentally without mention of *I. sparsa*. De Candolle's (in Redoute 1805) *I. liliago* is undoubtedly also subsp. *fimbriata* and was recognized by Ker Gawler (1818) as *S. fimbriata* var. *liliago* and by Robert Sweet (1826b) as *S. liliago*. Specimens in the Linnean Herbarium labeled *Ixia lacera* (a name not published by Linnaeus) are the basis for the nomen nudum *I. lacera* listed by Ker Gawler (1804a; in Sims 1802) and Roemer & Schultes (1817). Yet one more synonym was provided by Sweet (1830), *S. grandiflora* var. *striata*, based on a fine painting of subsp. *fimbriata* in *Curtis's botanical magazine*, vol. 20: t. 779 (Ker Gawler 1804b) where it was named *S. grandiflora* var. β. The epithet *striata* alludes to the dark streaks on the reverse of the tepals, a feature somewhat more pronounced in this painting than usually seen in the wild. It is obvious from the quality of the paintings of subsp. *fimbriata* published in 19th century Europe that the plant responded well to greenhouse culture and produced blooms as large as those in the wild. Subsp. *fimbriata* is seldom seen in gardens today, which is a pity, for it makes an attractive rock garden and container subject.

Representative specimens

WESTERN CAPE.—**3218** (Clanwilliam): Piketberg Mtns, Kapteins Kloof, N end in renosterveld, (–DA), 20 Sept. 1974, *Goldblatt 2721* (MO); Piketberg, wet, sandy slope E of Farm Weltevrede, (–DA), 19 Sept. 2007, *Goldblatt 13009* (MO); waterlogged vlei S of Farm Concordia N of Piketberg, (–DB), 27 Sept. 1981, *Goldblatt 6392* (MO). **3318** (Cape Town): Mud River road, W of Mamre–Darling road, (–AD), 19 Sept. 1981, *Goldblatt 6284* (MO); between Porterville and Twenty Four Rivers, (–BB), 20 Aug. 1976, *Goldblatt 3922* (MO); Groenekloof (–CB), *H. Bolus 4344* (BOL); Cape Peninsula, Signal Hill (–CD), *Barker 453* (NBG), *Wolley Dod 579* (BOL); Tygerberg Nature Reserve, heavier soils in higher places, (–DC), *Loubser 3024* (MO); Stellenbosch, (–DD), *Strey 495* (PRE). **3319** (Worcester): near Wellington, (–AC), 15 Aug. 1926, *Grant 2368a* (MO).

Unverified locality: **3318** (Clanwilliam): near Graafwater on Lutzville Road, L/H side of road in sandy loam soil, (BA), 3 Sept. 1953, *Van Breda 869* (PRE).

6b. subsp. **grandiflora**.

Ixia uniflora L.: 27 (1767). Type: South Africa, without precise locality or collector (*LINN58/19*, holo.!).

Ixia holosericea Jacq.: 9 (1797). Type: South Africa, without precise locality or collector, illustration in Jacq.: t. 17 (1797).

Ixia aristata var. *atropurpurea* [Ker Gawl in] Andrews: t. 87 (1800). Type. South Africa, without precise locality or collector, illustration in Andrews: t. 87 (1800).

Sparaxis meleagris Eckl.: 27 (1827). Type: unknown.

Sparaxis stellaris D.Don in Sweet: t. 383 (1837). *S. grandiflora* var. *stellaris* (D.Don) Baker: 99 (1877). Type: South Africa, without precise locality or collector, illustration in Sweet: t 238 (1837).

Sparaxis atropurpurea Klatt: 389 (1882), nom. superfl. pro *Ixia holosericea* Jacq. Type: South Africa, [Western Cape], Tulbaghskloof, *Zeyher s.n.* [B—Herb. Lubeck, lecto.!, designated by Goldblatt: 240 (1969)].

Illustrations: Manning *et al*.: 358 (2002).

Plants mostly 150–200 mm high. *Leaves* lanceolate, acute to acuminate, up to 10 mm wide, lower sometimes falcate. *Flowers* deep red-purple but white in throat and tube (rarely whitish, sometimes flushed or speckled purple inside and outside); tepals spathulate, obtuse, 25–30 × 8–18(–25) mm, spreading ± horizontally when fully open. *Stamens*: anthers 10–12 mm long. *Style branches* ± 7 mm long. Plate 2D.

Distribution: essentially restricted to the Tulbagh Valley, with a single collection from Voëlvlei just west of the Elandskloof Mountains and outside the Tulbagh Valley, subsp. *grandiflora* occurs in lowland, now largely given over to agriculture (Figure 10). Plants persist locally along roadsides and in undisturbed renosterveld between Tulbagh and Wolseley. Plants grow in heavy clay, which may become inundated in seasons of above average rainfall. Burning or clearing of the veld stimulates flowering.

Subsp. *grandiflora* is pollinated, as far as we know, only by hopliine beetles and the only hopliine we have captured on the flowers is *Peritrichia rufotibialis*. The intense plum-red, radially symmetric perianth with pale throat is consistent with this pollination system (Goldblatt *et al*. 1998; Goldblatt & Manning 2011).

Despite its attractive flower, subsp. *grandiflora* is rarely seen in cultivation today and we suspect it is less amenable to horticulture than its congeners like *Sparaxis tricolor* and the range of *Sparaxis* hybrids available in the nursery trade. Nevertheless, it is a very desirable plant for the container or rock garden.

Conservation status: EN (Endangered), the subspecies has lost much of its original range, and although it was once common in the Tulbagh Valley it is difficult to find viable populations today.

Diagnosis: subsp. *grandiflora* is immediately recognized by the dark, plum-red flower colour, unique in the Iridaceae. Occasional albino morphs have been recorded among the purple. The flowers are also distinctive in the spathulate tepals that spread almost horizontally when fully open. A pale throat and white pollen provide an unexpected contrast to the darkly pigmented tepals. Vegetatively subsp. *grandiflora* closely matches subsp. *fimbriata*, which occurs in similar habitats on the coastal plain west of the mountains that isolate the Tulbagh Valley. The two subspecies appear to intergrade around Voëlvlei near Gouda at the western foot of the Elandsberg Mountains.

History: subsp. *grandiflora* must have been in cultivation in Europe at least as early as the 1760s, where its brilliantly coloured and relatively large flowers would have attracted considerable attention. Although first described by D. Delaroche in 1766 from plants grown in Holland, it later acquired several synonyms, most notably *Ixia holosericea* (Jacquin 1797), the name of which was arbitrarily changed by Klatt in *Sparaxis* (1882) to *S. atropurpurea*. The species was named *I. aristata* var. *atropurpurea* in 1800 by Ker Gawler, who later realized that *Ixia aristata* Thunb. was an entirely different plant and that at species rank his variety had already been described more than once. The name *I. aristata* was first misapplied to subsp. *grandiflora* by Aiton (1789), the source of Ker Gawler's later error. *I. aristata* is a later synonym of *Ixia latifolia* D.Delaroche. Ker Gawler (1804a) provided the transfer of Delaroche's *Ixia grandiflora* to *Sparaxis*.

Representative specimens

WESTERN CAPE.—**3319** (Worcester): between Tulbagh and Wolseley, stony clay, (–AC), 8 Sept. 1976, *Goldblatt 4079* (MO) (some plants with white flowers); Boontjiesrivier road, near Wolseley, heavy clay in renosterveld, (–AC), 26 Aug. 2000, *Goldblatt 11427* (MO); moist places in veld near Tulbagh, (–AC), 11 Sept. 1926, *Grant 2470* (MO, PRE); Tulbagh, (–AC), *Ecklon & Zeyher Irid 112* (77.9) (MO, TCD); Artois, (–AC), *Compton 11677* (NBG), *Esterhuysen 6080* (BOL); Steendal, Tulbagh, (–AC), *MacOwan 583* (BOL, SAM).

6c. subsp. **acutiloba** *Goldblatt* in Journal of South African Botany 35: 245 (1969) [description], Flora of Southern Africa 7(2), part 1: 163 (1999) [citation of type material]. Type: [Western Cape]: 8 miles [± 12 km] south of Clanwilliam, wet clay, 28 Aug. 1968, *Goldblatt 264* (BOL, holo.!; MO. iso.!).

?*Ixia monanthos* D.Delaroche: 21 (1766). *Sparaxis monanthos* (D.Delaroche) N.E.Br.: 135 (1929). Type: South Africa, without precise locality or collector (G—Herb. Burman, holo.!).

Sparaxis lutea Eckl.: 28 (1827). Type. South Africa, without precise locality, ex Hort. Ludwig, *Ecklon s.n.* (S, holo.!).

Illustrations: Manning *et al*.: 358 (2002); Le Roux *et al*.: 52 (1981)

Plants mostly up to 350 mm high, rarely to 450 mm. *Leaves* sword-shaped to almost linear, acute to acuminate, ± two thirds as long as stem, mostly 6–10 mm wide. *Flowers* bright yellow, bases of tepals with a small to prominent purple-black spot, sometimes flushed mauve on reverse of tepals, especially outer, faintly sweet-scented; tepals narrowly oblanceolate to obovoid, acute to subobtuse, 24–30 × 12–14 mm. *Stamens*: anthers 9–10 mm long. *Style* dividing opposite lower to upper third of anthers, branches ± 6 mm long. Plate 3A.

Distribution: found only in the Olifants River Valley, subsp. *acutiloba* is restricted to exposures of Bokkeveld shales in this area of predominantly Cape Sandstone-derived soils. Populations have been recorded only from the central part of the valley, from Citrusdal to some 10–12 km south of Clanwilliam, all at fairly low elevations along the valley bottom (Figure 10).

Conservation status: LC (Least Concern), but we note that populations near Citrusdal are threatened by urban expansion; elsewhere populations are currently stable but vulnerable to expansion of the N7 road alongside which it grows.

Diagnosis: subsp. *acutiloba* is recognized by the bright, clear yellow flowers with comparatively narrow, oblanceolate to narrowly obovate tepals mostly 24–30 × 12–14 mm and the relatively narrow leaves, mostly 6–10 mm wide. The tepals remain ascending and the flower is thus more-or-less cup-like even when fully open.

History: the earliest collection of subsp. *acutiloba* may be a specimen at the Delessert herbarium, Geneva, the type of *Ixia monanthos* (Delaroche 1766), but we are uncertain of the identity of the plant owing to its condition today. The plant illustrated in *Curtis's botanical magazine* vol.15, t. 545 (1802) and misidentified as *Ixia bulbifera* is evidence that subsp. *acutiloba* was in cultivation in Europe during this period. Another early collection dating from the 1820s at the Stockholm Herbarium was made by C.F. Ecklon from plants cultivated at Baron Ludwig's garden in Cape Town. Only in 1894 was the wild locality of the subspecies established when Rudolf Schlechter encountered plants in the Olifants River Valley.

Representative specimens

WESTERN CAPE.—**3218** (Clanwilliam): between Clanwilliam and Citrusdal at Algeria turnoff, (–BD), 25 Aug. 1974, *Goldblatt 2438* (MO); 1 mile [± 1.5 km] from Alpha on Algeria road, (–BD), *Gillett 4133* (BOL, K). **3220** (Wuppertal): Citrusdal, Loop Street, vacant plot, (–DA), 8 Sept. 1995, *Hanekom 2773* (MO, NBG); 5 miles [±7.5 km] N of Citrusdal, (–DA), *Barker 3606* (NBG), *Compton 20764* (NBG); northern outskirts of Citrusdal on old road to Clanwilliam, (–DA), 13 Sept. 1981, *Goldblatt 6270* (MO). Without precise locality: Olifants River Valley, 166 m, 24 Aug. 1894, *Schlechter 4990* (BOL, MO, Z).

6d. subsp. **violacea** (Eckl.) Goldblatt in Journal of South African Botany 35: 244 (1969). *Sparaxis violacea* Eckl.: 27 (1827). Type: South Africa, [Western Cape], Bot River, *Ecklon & Zeyher Irid 114* (SAM, lecto.!, designated by Goldblatt: 244 (1969); MO, isolecto.!).

Sparaxis cana Eckl.: 28 (1827). Type: South Africa, without precise locality, ex Hort. Ludwig, Cape Town, *Ecklon s.n.* (S, holo.!).

Illustrations: Manning *et al*.: 358 (2002).

Plants rarely more than 200 mm high, sometimes only 60 mm high (*Goldblatt 4094*), usually unbranched. *Leaves* often markedly falcate to lanceolate, ± 1/3 to 1/2 as long as stem, obtuse acuminate or acute, 6–12 mm wide, margins slightly thickened and sometimes turning purple. *Flowers* pale violet with white throat and tube or ± white, then often with violet spots at tepal bases, tepals flushed grey-mauve on reverse, especially outer tepals, strongly scented of freesia; tepals spathulate, obtuse, 22–37 × 7–16 mm. *Stamens*: anthers up to 7 mm long. Plate 3B

Distribution: occurring across the low, rolling hills of the Overberg, subsp. *violacea* extends from Bot River in the west to Fairfield, near Napier in the east (Figure 10). It occurs in much the same habitats as the other subspecies of *S. grandiflora*, namely clay slopes in renosterveld. The flowers we have examined alive have a surprisingly strong scent of freesia, which likely signifies pollination by large bees, but there are no recorded observations of its pollination.

Conservation status: LC (Least Concern), but we strongly suggest VU (Vulnerable)—with the intensive cultivation of cereal crops, much of its original habitat is now lost, and road verges often sprayed with weed killer have eliminated it from many relict colonies. We know of no reserve within its range where it is protected in any way, but it persists as small colonies locally on banks where the ground is too steep to plough.

Diagnosis: subsp. *violacea* is recognized by the pale violet to white flowers with markedly spathulate tepals. It tends to be less robust than the other subspecies, plants seldom exceeding 200 mm high, with distinctly shorter and broader leaves with somewhat thickened margins. The strong freesia-like odour of the flowers is unique among the subspecies, which have unscented or at best very faintly scented blooms.

History: subsp. *violacea* appears to have first been collected by C.F. Ecklon and C.L. Zeyher in the 1820s near Bot River, west of Caledon. Ecklon provided the name *Sparaxis violacea* in 1827. *Sparaxis cana*, which was described by Ecklon at the same time, represents the white-flowered morph of the subspecies. The plants were in cultivation in Cape Town at the time that Ecklon described *S. cana* and *S. violacea*.

Representative specimens

WESTERN CAPE.—**3419** (Caledon): SW of Villiersdorp, Queen Anne Farm, Klipfontein 82, (–AA), 20 Sept. 2001, *Oliver & Oliver 11943* (NBG); clay slopes on road from Bot River from main Villiersdorp road, (–AA), 1 Sept. 1976, *Goldblatt 4005* (MO); road to Franschhoek, 18 miles [27 km] from Caledon, (–AA), 30 Sept. 1971, *Barker 10846* (NBG); between Theewater River bridge and Eseljag pass, clay slopes recently burned, (–AA), *Goldblatt 2500* (MO); Caledon, commonage E of town, (–AB), 13 Sept. 2009, *Goldblatt & Manning 13443* (MO, NBG); Hemel-en-Aarde Valley, 4 km E of Shaw's Pass, (–AD), 13 Sept. 1976, *Goldblatt 4094* (MO); between Lindeshof and Greyton, (–BA), 24 Sept. 1959, *Lewis 5662* (NBG). **3419** (Bredasdorp): Fairfield, (–BC), 29 Aug.1958, *Lewis 5283* (NBG).

7. **Sparaxis bulbifera** *(L.) Ker Gawl*. in Annals of Botany (König & Sims) 1: 226 (1804a). Baker: 116 (1896, excluding *S. grandiflora* subsp. *violacea* as var. β, *violacea*). *Ixia bulbifera* Mill. ex L.: 4 (1756). *Belamcanda bulbifera* (L.) Moench: 214 (1802, as *Belemcanda*). *Pardanthus bulbiferus* (L.) Klatt: 551 (1862). Type: South Africa, without precise locality or collector [LINN 58/16, neo.!, designated by Goldblatt: 237 (1969)].

Ixia alba L.: 862 (1759). Type: unknown. Said by G.J.Lewis: 185 (1962) to be *S. bulbifera* without explanation.

Ixia bulbifera Mill.: (1768), illegitimate homonym, not *I. bulbifera* L. (1756). Type: South Africa, without precise locality or collector, illustration in Miller: t. 236, f. 2 (1758).

Sparaxis albiflora Eckl.: 28 (1827). Type: South Africa, without precise locality, *Zeyher s.n.* [SAM, lecto designated by Goldblatt: 237 (1969)].

Sparaxis miniata Klatt: 389 (1882). Type: South Africa, without precise locality, *Drège 3968* (S, holo.!).

Plants 150–300(–500) mm high, usually with up to three branches from aerial nodes, after flowering bearing several small cormlets at each aerial node as well as below ground. *Corm* 9–15 mm diam., tunics of fine pale fibres. *Leaves* 5–9, narrowly sword-shaped, acute, both basal and cauline, reaching to ± base of spike, 4–11 mm wide, closely veined with prominent main vein. *Spike* fairly lax, flexed below base of first flower, mostly 2–4-flowered; bracts dry, crinkled, uniformly pale or streaked with brown, outer mostly 14–16 mm long, with 3 subequal cusps slightly longer than body of bract, loosely twisted, inner bracts similar but slightly shorter, 2-cusped. *Flowers* with radially symmetric perianth but unilateral stamens, white but yellow in throat and tube, sometimes with small black spot at base of each tepal, outer tepals often purple outside, usually faint sweet rose-scented; perianth tube funnel-shaped, 14–16 mm long, narrow basal part 5–7 mm long; tepals subequal, narrowly ovate to lanceolate, 25–28 × ± 12 mm. *Stamens* unilateral but not parallel, abaxial stamen twisted to lie against adaxial tepal, filaments 7–8 mm long, anthers facing centre of flower, 7–8 mm long, white; pollen white. *Style* unilateral, lying against adaxial tepal, white, dividing at or up to 2 mm beyond anthers tips, branches filiform, ± 10 mm long. *Capsules* ovoid to oblong, usually barrel-shaped, ± 8 × 6 mm with 9–10 seeds per locule, or oblong, ± 11 × 5 mm long with 11 or 12 seeds per locule. *Seeds* globose, ± 2 mm diam., glossy brown. *Flowering time*: mainly September to mid-October, occasionally in August. Figure 11, Plate 3C.

Illustrations: Manning & Goldblatt: 66 (1996); Manning *et al*.: 20 & 356 (2002).

Distribution and biology: widespread in the southwestern and southern Cape, *Sparaxis bulbifera* extends from Hopefield and Saldanha Bay in the west to Bredasdorp in the east, occurring on flats and the lower slopes of hills and mountains (Figure 12). Plants favour sandy ground, waterlogged in winter, but may also occasionally be found on wet clay soils. In disturbed sites *S. bulbifera* can be found in masses, then providing a striking display for a few weeks, as at Kenilworth Race Course in Cape Town. The species is occasionally seen as a container subject and responds well when provided with ample nutrients and water. It is not much cultivated, and perhaps this is good given its propensity for ample vegetative propagation via the numerous cormlets borne on the aerial nodes. A plant of sandy soils, its corms are often eaten by molerats. These animals often carry corms to nests for future consumption—survival of the genotype is assured by cormlets that fall on the ground or in the underground molerat runs.

Conservation status: LC (Least Concern).

Pollination of *Sparaxis bulbifera* is generalist, evidently a derived condition. Hopliine beetles, halictid bees and honey bee workers are frequently seen visiting the flowers. According to Horn (1962) the species is self-compatible, but capsules are seldom produced unless pollen transfer is facilitated by hand or insects. This is because the style branches are held above the anthers during anthesis, and even as the flower wilts, pollen and stigmatic surfaces seldom come into contact. Our own observations from plants collected at Kenilworth Racecourse and grown in the greenhouse show that they produce smaller than normal capsules containing few seeds when isolated from insect visitors.

FIGURE 11.—*Sparaxis bulbifera*, Rondebosch Common, without voucher. A, flowering plant; B, half-flower; C, outer (left) and inner (right) bracts; D, infructescence; E, seed. Scale bar: A, B, D, 10 mm; C, 5 mm; E, 2 mm. Artist: J.C. Manning.

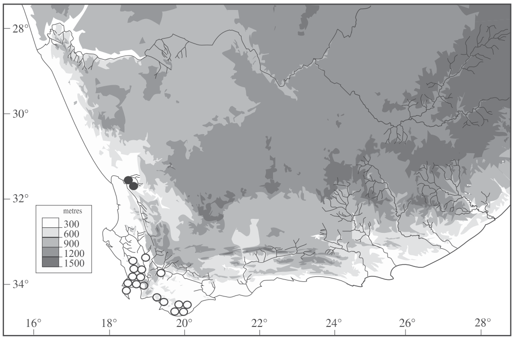


FIGURE 12.—Distribution of *Sparaxis bulbifera*, ○; *S. auriculata*, ●.

Diagnosis and relationships: the large white flowers of *Sparaxis bulbifera* are easily confused with those of white-flowered *S. grandiflora* subsp. *fimbriata*, and they are indeed strikingly similar in their radially symmetric perianth but unilateral stamens and unilateral style with long slender style branches. Careful examination of the flowers shows that the abaxial stamen (i.e. opposite the floral axis) curves back across the centre of the flower to lie against the adaxial tepal (i.e. nearest the floral axis) (Figure 11). The tepals of *S. bulbifera* are narrowly ovate to lanceolate, whereas those or *S. grandiflora* subsp. *fimbriata* tend to be broader, usually widest in the upper third and sometimes spathulate. The two species are easily distinguished by vegetative features: *S. grandiflora* produces branches from the base; thus close to or below ground level, whereas branching in *S. bulbifera* is aerial and even when unbranched, the stems of this species have one or more aerial nodes, each bearing a leaf, and after flowering a cluster of small cormlets—a feature that is not present in *S. grandiflora*. This easy distinction has not, however, prevented the two species from being confused. The differences in habitat also help separate the two: *S. grandiflora* favours clay ground, sometimes waterlogged in winter but relatively well drained, whereas *S. bulbifera* is rarely encountered away from wet, sandy flats. The two species are evidently immediately related (Figure 1a, b), and, not surprisingly, hybrids between the two have been recorded, for example, at Tygerberg Nature Reserve, where their habitats overlap (*Loubser 3057* MO).

History: a common plant on the Cape Peninsula and nearby, *S. bulbifera* was known in Europe shortly after the Dutch settlement was established at the Cape in the 1650s. It was described by Carl Linnaeus in 1756 but was known in Great Britain earlier than this. Plants grown for Phillip Miller at the Chelsea Physic Garden were later painted and illustrated in his *Figures of Plants described in the Gardeners Dictionary*. The fascicle with the illustration was published in 1758, two years after Linnaeus described *Ixia bulbifera*. Significantly, Linnaeus cited Miller by name in the protologue but without elaboration. We are left wondering whether Miller provided Linnaeus with corms so named, possibly then grown in Sweden, or perhaps a draft of the text that accompanied the painting. There is reason to doubt, however, that the present specimen in the Linnean Herbarium is the one originally seen by Linnaeus (Goldblatt 1969). The only specimen in the collection today was designated a neotype by Goldblatt. Miller evidently considered *Ixia bulbifera* his own species and when he first used binomial nomenclature in the 1768 edition of *The Gardeners Dictionary*, he used the name without reference to Linnaeus. Miller's *Ixia bulbifera* is now regarded as an illegitimate homonym. Illustrations of *Sparaxis bulbifera* appeared occasionally in the scientific literature after the 1750s, for example, in Redouté's *Les Liliaceés* t. 128 (1805) [as *Ixia bulbifera*]. The painting in *Curtis's botanical magazine* t. 545 (1802), also identified as *I. bulbifera*, the sulphur-coloured *Ixia*, is *S. grandiflora* and most likely subsp. *acutiloba*.

Representative specimens

WESTERN CAPE.—**3318** (Cape Town): between Bokbaai and Darling, (–AB), *Esterhuysen 4375* (BOL); Darling, sandy places, (–AC), *Grant 2538* (BOL, MO); Wynberg Hill (–CD), Sept. 1950, *Pillans 10155* (MO); mountain sides near Cape Town, (–CD), Sept., *Ecklon & Zeyher Irid 119* (64.9) (MO); Paarl, Paardeberg, (–DD), *Salter 7665* (BOL); Muldersvlei, damp sandy ground, (–DD), 6 Oct. 1955, *Lewis s.n.* (MO, SAM 68310). **3319** (Worcester): wet roadside beyond Voëlvlei, in wetter sites, (–AC), 13 Sept. 1978, *Goldblatt 4869* (MO); near Worcester, (–CB), *Walters 194* (NBG). **3418** (Simonstown): Oatlands Point, (–AB), *Wolley Dod 2855* (BOL, PRE); Cape Flats, (–BA), Sept. 1892, *Schlechter 1558* (Z); sandy flats near Gordon's Bay, (–BB), *Parker 4239* (NBG). **3419** (Caledon): Onrus River, sandy ground near the sea, (–AC), 24 Sept. 1936, *Gillett 4396* (BOL, K); Hermanus, Mossel River shore, (–AD), *Compton 2362* (NBG); Ratel River, near homestead, (–DA), 29 Sept. 1970, *Goldblatt 335* (BOL); west of Elim, (–DA), *Muir 5020*

(NBG); Farm Springfield, (–DB), 15 Sept. 1984, *Albertyn 559* (MO). **3420** (Bredasdorp): Bredasdorp, (–CA), *Van Breda 713* (PRE).

Without precise locality: Clanwilliam, banks of the Olifants river and Villa Brakfontein, *Ecklon & Zeyher Irid 116* (76) (MO, TCD)

8. **Sparaxis fragrans** *(Jacq.) Ker Gawl.* in Annals of Botany (König & Sims) 1: 225 (1804a). Baker: 117 (1896). Goldblatt: 235 (1969). *Ixia fragrans* Jacq.: t. 274 (1794a). *Romulea fragrans* (Jacq.) Eckl.: 19 (1827). *Gladiolus odorus* Schrank: 206 (1822), as a new name for *Ixia fragrans* Jacq. (1794a), not *G. fragrans* Jacq. (1797) and also an illegitimate homonym, not *G. odorus* Salisb. (1796). Type: South Africa, Western Cape, without precise locality, illustration in Jacq.: t. 274 (1794a).

Ixia sordida Hornem.: 6 (1819). Type: South Africa, without precise locality, cultivated in Copenhagen, Denmark, *Horneman s.n.* (C, holo.!).

Synnotia stenophylla Baker: 865 (1901). Type: South Africa, [Western Cape], *Ecklon & Zeyher Irid. 118* (Z, holo.! [with misplaced flower of *S.* cf. *metelerkampiae*]; PRE!, SAM!, TCD!, iso.).

Plants mostly 100–200 mm high, stem usually unbranched, or with a branch produced from base, with small cormlets in underground leaf axils. *Corm* globose, ± 15 mm diam., tunics of fine, pale fibres extending upward as collar around stem base. *Leaves* 6–10, all ± basal, reaching to ± base of spike, narrowly sword-shaped to sublinear, 2–9 mm wide, obtuse, obliquely apiculate, closely veined with ± prominent central vein. *Spike* slightly inclined, 1–3(4)-flowered, weakly flexuose, flowers spirally arranged; bracts dry, crinkled, translucent with light brown streaks, 15–18 mm long, lateral margins fimbriate, distally drawn into long tapering cusps, outer 3-veined and 3 prominently 3-cusped, inner 2-veined and 2-cusped, cusps often twisted or coiled. *Flowers* radially symmetric, pale to deep yellow to pale beige, often flushed brown or grey-purple on reverse of outer tepals, occasionally with small black spot near tepal bases, sweetly or unpleasantly sour smelling; perianth tube funnel-shaped, 6–8 mm long, narrow basal part ± 4 mm long; tepals subequal, ± oblong, 18–25 × ± 7 mm. *Stamens* symmetrically arranged, filaments erect, ± 6 mm long, enclosing style, anthers contiguous below, diverging above, 6–9 mm long, pale yellow. *Style* dividing opposite upper third of anthers, branches filiform below, gradually expanded and recurved in distal half, ± 5 mm long, extending outward between upper third of anthers. *Capsules* ± globose, 9–10 × ± 7 mm. *Seeds* light brown, up to 6 per locule, ± 2 mm diam. *Chromosome number* $2n = 20$. *Flowering time*: mid-August to late September. Figure 13, Plate 3D.

Illustrations: Manning *et al.*: 357 (2002).

Distribution and biology: endemic to the Caledon District in the southwestern Cape, *Sparaxis fragrans* extends from Bot River and Villiersdorp in the west to the end of the Caledon Swartberg in the east (Figure 14). Plants favour clay flats and slopes, often waterlogged in the winter months. The yellow, often somewhat unpleasantly scented flowers are pollinated by a range of small insects including halictid bees, native honey bees (*Apis mellifera*), and the hopliine beetle, *Platychelus* sp. (Goldblatt *et al.* 2000). All captured insects carried loads of pure *Sparaxis* pollen. Both pollen and traces of sweet nectar are rewards for bee visitors.

Conservation status: VU (Vulnerable), but we suggest EN (Endangered) as much of it range is lost to agriculture and alien vegetation and the species persists locally on road verges and steep banks.

Diagnosis and relationships: *Sparaxis fragrans* is recognized by the small yellow to buff, mostly unpleasantly scented flowers with symmetrically disposed stamens, and narrow, acute leaves. It shares virtually identical, fringed bract margins and radially symmetric flowers with the closely related *S. maculosa*, but the latter has larger, unscented blooms boldly marked at the base of the tepals with large maroon-purple markings divided longitudinally by a pale yellow line.

History: the first collection of *Sparaxis fragrans* to reach western Europe was probably made by Franz Boos and Georg Scholl, who were commissioned to send collections of Cape plants to Vienna where many were grown and flowered. The species appeared in fascicle 15 of Jacquin's *Icones plantarum rariorum* in 1794 under the name *Gladiolus fragrans* and was transferred by Ker Gawler in 1804 to his new genus *Sparaxis*. It was cultivated in Copenhagen, Denmark, some years later, possibly from the Vienna

FIGURE 13.—*Sparaxis fragrans*, *Goldblatt & Porter 12992*. A, flowering plant; B, half-flower; C, outer (upper) and inner (lower) bracts. Scale bar: A, B, 10 mm; C, 5 mm. Artist: J.C. Manning.

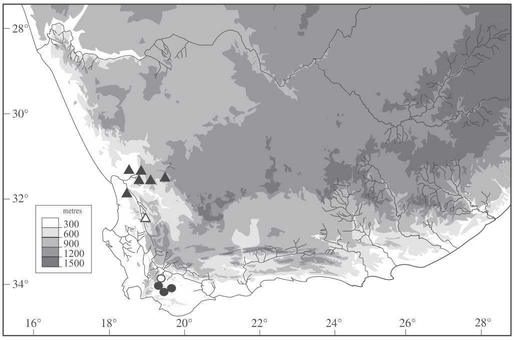


FIGURE 14.—Distribution of *Sparaxis maculosa*, ○; *S. fragrans*, ●; *S. roxburghii*, Δ; *S. galeata*, ▲.

stock, and named *Ixia sordida* by the Danish botanist Jens Horneman in 1819, evidently in ignorance of Jacquin's earlier published name. *Sparaxis fragrans* was collected in the late 1820s by C.F. Ecklon and C.L. Zeyher, who established its native range, until then unknown, in the Caledon District.The species was not collected again, as far as we can establish, until over 140 years later when it was found in the low hills between Caledon and Bot River.

Representative specimens

WESTERN CAPE.—**3419** (Caledon): 10 km SW of Villiersdorp, 0.5 km N of Rooidak on Bot River 106, (–AA), 19 Sept. 2001, *Helme 2244* (NBG); N of Bot River, (–AA), 30 Aug. 1968, *Barker 10575* (NBG); N of Bot River near Farm Goedvertrou, (–AA), 16 Aug. 1997, *Goldblatt & Manning 10670* (MO); Zwartberg, Caledon, (–AB), without date, *Ecklon & Zeyher Irid 118* (SAM, PRE, Z); Van der Stel's Pass, Farm Welgemoed, 15 Sept. 2007, *Goldblatt & Porter 12992* (NBG); 7 km E of Bot River, Die Vlei Siding, renosterveld, (–AB), 30 Aug. 2001, *Helme 2022* (NBG); Farm Vleitjies, Caledon to Villiersdorp, (–AB), 3 Sept. 1982, *Burgers 2908* (NBG); Farm Swartrivier, N side of Caledon Swartberg, (–AB), 11 Sept. 1980, *Goldblatt 5781* (MO); clay slopes of Caledon Swartberg, on detour Drayton to Greyton turnoff, (–BA), 14 Sept. 1978, *Goldblatt 4878* (MO), 31 Aug. 1976, *Goldblatt 3995* (MO).

9. **Sparaxis maculosa** *Goldblatt* in Annals of the Missouri Botanical Garden 79: 153 (1992). Type: [Western Cape], Farm Stettyn, between Worcester and Villiersdorp, 8 Sept. 1988, *Perry & Manning 3603* (NBG, holo.!; K!, MO!, NBG!, PRE!, iso.).

Plants 100–200(–300) mm high, stem simple or 1- or 2-branched from base. *Corm* globose, ± 15 mm diam., tunics of fine pale closely matted fibres. *Leaves* 7–9, ± basal, ± two thirds as long as spike, lanceolate(–oblong), 9–12 mm wide, abruptly expanded adaxially above sheath, obliquely apiculate, closely veined with ± prominent central vein. *Spike* 1–2(–3)-flowered, weakly flexuose, flowers spirally arranged; bracts dry, crinkled, translucent with brown streaks, lateral margins fimbriate, 15–20 mm long, distally drawn into long tapering cusps, outer with 3 prominent veins, 3-cuspidate, inner with 2 prominent veins and 2-cuspidate. *Flowers* actinomorphic, bright yellow, tepals each with dark maroon-purple, heart-shaped mark with central yellow streak in lower third, unscented; perianth tube funnel-shaped, 6–7 mm long, narrow basal part ± 2.5 mm long; tepals subequal, ± oblong, 27–35 × 8–10 mm. *Stamens* symmetrically arranged, filaments erect, 6–7 mm long, anthers linear, diverging, contiguous below, 9.5–11.0 mm long, pale yellow. *Ovary* globose, ± 2.5 mm long, style dividing opposite the lower third of anthers, branches filiform, 4.5–5.0 mm long, extending outward between upper third of anthers. *Capsules* ± globose, shortly stipitate on stalks ± 1 mm long, 6–9 × 5–6 mm, not splitting at apex, walls eventually fragmenting by horizontal cracks. *Seeds* reddish brown, up to 8 per locule, ± 2 mm diam. *Chromosome number* unknown. *Flowering time*: late August and September. Figure 15, Plate 4A.

Distribution and biology: discovered only in 1988, *Sparaxis maculosa* is known from just a few farms in the Stettyn area of the Hoeks River drainage north of Villiersdorp (Figure 14). Plants grow in heavy clay in renosterveld and are today seriously endangered by expanding agriculture. It seems likely that *S. maculosa* originally consisted of a single extended population, but just three fragmentary colonies of the species are known to us today. It is likely that the flowers are adapted for hopliine beetle pollination, given the conspicuous dark markings of the flowers and their lack of scent, but there are no observations on pollination of the species. Compatibility relations are likewise unknown.

Conservation status: CR (Critically Endangered).

FIGURE 15.—*Sparaxis maculosa*, *Perry & Manning 3603*. A, flowering plant; B, outer (upper) and inner (lower) bracts. Scale bar: A, 10 mm; B, 5 mm. Artist: J.C. Manning.

Diagnosis and relationships: *Sparaxis maculosa* is recognized by the radially symmetric yellow flowers with a dark centre and long-cuspidate bracts with the lateral margins slightly and irregularly serrated. The bracts are almost identical to those of *S. fragrans*, which also has a radially symmetric flower. There is no doubt that the two are immediately related and there was initially some question as to whether they were distinct (Goldblatt 1992). *S. fragrans* is, however, consistently a more slender plant with linear to narrowly lanceolate (or falcate) leaves, 2–8 mm wide and predominantly yellow to buff flowers with narrower tepals, ± 7 mm wide, sometimes with small dark marks at the tepals bases. The flowers of *S. fragrans* mostly have a slightly unpleasant, acrid odour whereas we have found those of *S. maculosa* lacking scent.

The broader relationships of *Sparaxis maculosa* and *S. fragrans* are with sect. *Sparaxis*, but the molecular phylogenies (Figure 1a, b) show the species pair to be phylogenetically isolated with no close allies.

Representative specimens

WESTERN CAPE.—**3319** (Worcester): Hoeks River valley, flats near Farm Stettyn, (–CD), 6 Sept. 2002, *Goldblatt & Porter 12169* (MO, NBG); Farm Stettyn, clay ground, (–CD), 14 Sept. 1989, *De Vos 2713* (NBG).

10. **Sparaxis auriculata** *Goldblatt & J.C.Manning* in Bothalia 29: 59 (1999). Type: South Africa, [Western Cape], Farm Keurlandshoek (Colinshoek), slopes of the Gifberg, 7 Aug. 1998, *Goldblatt & Manning 10966* (NBG, holo.!; K!, MO!, PRE!, S!, iso.).

Plants 150–400 mm high, stem usually 1- or 2-branched from axils of cauline leaves, inclined above. *Corm* globose-conical, 12–14 mm diam., tunics of medium-textured fibres mostly oriented vertically. *Leaves* 5–8, mainly basal, uppermost inserted in middle of stem, reaching to between middle of stem and base of spike, narrowly lanceolate, acute, mostly 10–15 mm wide, with prominent submarginal vein, margin thus appearing somewhat thickened, sheathing parts of leaves speckled with purple (often fading when dry). *Spike* mostly 5–7-flowered, weakly flexuose, ± secund; bracts pale below with whitish veins, becoming streaked with light brown above, 15–20 mm long, lightly lacerate with prominent central cusp, inner bracts slightly shorter, with 2 terminal cusps. *Flowers* zygomorphic, bilabiate, pale yellow, dorsal tepal pale mauve, lower tepals deep yellow fading to white at tips, abaxial half of throat obscurely lined with grey-purple, unscented; perianth tube obliquely funnel-shaped, distal part curving outwards, ± 18 mm long, lower tepals united for 6–7 mm, basal cylindrical portion narrow and clasping style; tepals unequal, dorsal largest, broadly ovate, erect, ± 25 × 18–20 mm, upper lateral tepals oblong-ovate, ± 20 × 10–12 mm, spreading distally, lower 3 tepals abruptly deflexed and pinched together at bases, directed downward, ± 18 × 8 mm, strongly channelled, lower laterals with prominent auricular lobes at base. *Stamens* unilateral and arcuate, filaments ± white, ± 18 mm long, anthers 7–8 mm long, creamy white, exserted, pollen creamy white. *Ovary* 3.5 mm long, oblong-trigonous, style arching over stamens, white, ± 4 mm long, dividing just below anther tips, branches filiform, diverging and recurved in distal half, slightly wider toward apex. *Capsules* ± barrel-shaped, trilobed, ± 6(–7) × ± 6 mm, showing outline of seeds. *Seeds* 3 or 4 per locule, ± 2.2 mm diam., glossy light brown. *Flowering time*: August to early September. Figure 16, Plate 4B.

Illustrations: Manning *et al*.: 356 (2002).

Distribution and biology: *Sparaxis auriculata* is a local endemic of the Gifberg–Matsikamma Mountain complex of northern Western Cape in the Vanrhynsdorp District (Figure 12). Plants have been recorded in rocky sites on sandstone at low to middle elevations and are locally common among rocks and in cleared places on bush-covered sandstone slopes. The flowers share the common pollination system of the genus, large bodied, long-tongued bees that visit the flowers to forage for nectar (Goldblatt *et al*. 2000).

Conservation status: EN (Endangered).

Diagnosis and relationships: the flowers of *Sparaxis auriculata* resemble those of the common southwestern Cape *S. villosa* in general appearance but are substantially larger in all respects. In *S. auriculata* the dorsal tepal is ± 25 × 18–20 mm and the anthers 7–8 mm long, compared with a dorsal tepal 14–19 × 10–12 mm and anthers 3–4 mm in *S. villosa*. Furthermore, the style in the latter species divides near the anther bases, the style branches are ± 3 mm long, rarely

FIGURE 16.—*Sparaxis auriculata*, *Goldblatt & Manning 10966*. A, flowering plant; B, flower, front view and half-flower; C, infructescence; D, seed. Scale bar: A–C, 10 mm; D, 2 mm. Artist: J.C. Manning.

reaching beyond the middle of the anthers, and the lower tepals are inclined slightly below the horizontal and without auriculate basal lobes, whereas *S. auriculata* has longer anthers, style branches ± 4.5 mm long and exceeding the anthers, and downward-directed lower tepals with prominent auricular lobes. *Sparaxis auriculata* can also be distinguished by its vegetative features. The corms are narrowly conic, have tunics of medium-textured fibres, the leaf sheaths are liberally spotted with dark purple, and the leaf blades are unique in *Sparaxis* in the prominent submarginal vein that makes the margins appear thickened. The corms of *S. villosa* differ substantially being globose with coarse, netted fibres, the vertical elements of which are thickened into claw-like ridges below, and the leaves lack the dark spotting so marked in *S. auriculata*.

The narrow, conical corms and soft corm tunics are characteristic of only two other species of *Sparaxis*, *S. galeata* and *S. roxburghii*—both northwestern Cape species. They have the underground part of the stem enclosed by a thick neck of fine fibres and also leaves with speckled sheaths. Both species differ from *S. auriculata* in floral details. *S. galeata* has short-tubed, extremely sweetly fragrant flowers with a reflexed dorsal tepal, and prostrate, obtuse leaves, and it favors dry, stony, clay flats and slopes. The rare *S. roxburghii* has long-tubed flowers (the tube 20–25 mm long), otherwise resembling those of *S. galeata*, and is known from a single population in the mid-Olifants River valley on stony slopes. Neither species has the submarginal vein of *S. auriculata*. The nuclear and combined nucelar plus plastid molecular phylogenies both place *S. roxburghii* as immediately related to *S. auriculata*.

History: *Sparaxis auriculata* appears to have first been recorded in 1979 by I.S. Walters at the farm Vleikraal (or Veekraal) on the slopes of the Gifberg east of Klawer. It was initially associated with the superficially similar *S. villosa*; then included in *Synnotia*. Gatherings made in 1997 and later on Gifberg Pass east of Vleikraal, where the type collection was made in 1998, show the species to be common locally.

Representative specimens

WESTERN CAPE. **3118** (Vanrhynsdorp): 4 km N of bottom of Gifberg Pass to Mauwerskop, (–CA), 18 Aug. 2001, *Helme 2125* (NBG); flats W of Matsikamma, 140 m, (–DB), 31 Aug. 1974, *Oliver 4990* (PRE); Farm Vleikraal E of Klawer, on E-facing lower slopes of the Gifberg, (–DB), Aug. 1979, *Walters 15* (NBG); Gifberg Pass, (–DB), 25 Aug. 1997, *Van Rooyen, Steyn & De Villiers 587* (NBG, PRU); Gifberg Pass, Keurlandshoek, (–DB), 25 Sept. 2008 (fr.), *Goldblatt & Porter 13178* (MO).

11. **Sparaxis roxburghii** *(Baker) Goldblatt* in Annals of the Missouri Botanical Garden 79: 156 (1992). *Synnotia bicolor* var. *roxburghii* Baker: 198 (1892); 135 (1896). *S. roxburghii* (Baker) G.J.Lewis: 146 (1956). Type: South Africa, [Western Cape], 15 miles [± 22 km] N of Citrusdal, 26 Aug. 1957, *Lewis 5207* (NBG, neo.!, designated by Goldblatt: 156 (1992); MO!, iso.). [The location of the original type, without precise locality, *Roxburgh s.n.*, is unknown].

Plants 280-450 mm high, stem often with 1(2) branches from aerial nodes. *Corm* 25-30 mm in diam., tunics of fine, netted fibers, extending upwards in collar around stem base. *Leaves* 7–9, all basal except uppermost, narrowly lanceolate, ± half as long as stem, 8–15 mm wide. *Spike* subsecund, mostly 5–7-flowered; bracts 15–20(–25) mm long, pale with brown streaks, margins lightly lacerate, outer with long central cusp, inner ± as long as outer, with 2 long cusps. *Flowers* zygomorphic, mauve to lilac, dorsal tepal darker than upper laterals, lower tepals yellow in lower two thirds tipped purple; perianth tube 20–30 mm long, cylindrical part 13–23 mm long, curved and expanding gradually distally, upper part funnel-shaped; tepals unequal, dorsal largest, lanceolate, 22–28 × 10–12 mm, upper laterals 18–20 × ± 8 mm, lower three smallest, joined for 6–7 mm, ± 13 mm × ± 5.5 mm. *Stamens* unilateral, arcuate, filaments 15–20 mm long, anthers 4–5 mm long, pollen yellow. *Ovary* ± 4 mm long, style dividing near anther bases, branches ± 4 mm long, spreading outwards, filiform. *Capsules* ± globose, 5–6 × ± 5 mm. *Seeds* 3(4) per locule, size unknown. *Flowering time*: late August to mid-September. Figure 17, Plate 4C.

Illustrations: Manning *et al*.: 360 (2002).

Distribution and biology. *Sparaxis roxburghii* is known with certainty from a single locality, a low ridge in the Olifants River Valley between Citrusdal and Clanwilliam, a short distance south of the bridge over the Olifants River at

FIGURE 17.—*Sparaxis roxburghii*, *Goldblatt & Manning 11009*. A, flowering plant; B, half-flower; C, outer (left) and inner (right) bracts; D, infructescence and detached capsule; E, seed. Scale bar: A, B, D, 10 mm; C, 5 mm; E, 2 mm. Artist: J.C. Manning.

Kriedoukrans and the road to Algeria and the Cedarberg (Figure 14). After repeated searches for the species, we located a small population in stony ground adjacent to a citrus orchard in 1998. This is close to where it was rediscovered by T.M. Salter in 1938 and later recollected by G.J. Lewis and W.F. Barker in the 1940s and 1950s. The last record before our own was made in 1957. The corms we collected were grown at Kirstenbosch National Botanical Garden where the large, colourful flowers made a striking display. Unfortunately the species is no longer in the living collection there.

The long-tubed flowers are almost certainly adapted for pollination by *Prosoeca peringueyi*, the common long-proboscid fly of the Olifants River Valley that is on the wing in August and September. The tube length, 20–30 mm, and mauve colouring with yellow nectar guides edged with dark purple are typical attributes of flowers pollinated by this nemestrinid fly (Manning & Goldblatt 1996).

Conservation status: CR (Critically rare) or, we suggest EN (Endangered) (Table 2), the rarest and most seriously threatened member of the genus. On-site investigation is needed to establish the population size.

Diagnosis and relationships: the finely fibrous corm tunics forming a neck around the stem base, and the erect to reflexed, rather than hooded, upper tepal suggest that *Sparaxis roxburghii* is most closely related to *S. galeata*, from which it is distinguished by the elongate perianth tube, 20–30 mm long vs ± 15 mm in *S. galeata*, and the differently coloured and proportioned flower. Molecular studies, however, suggest that *S. roxburghii* is most closely related to *S. auriculata*, which has a perianth tube ± 18 mm long, but funnel-shaped rather than largely cylindric. All three species have unusually small and nearly globose capsules containing only 2–4 seeds per locule.

History: described by J.G. Baker in 1892 as a variety of *Synnotia bicolor* (i.e. *Sparaxis villosa*), *S. roxburghii* was distinguished from typical *S. bicolor* by its finely fibrous corm tunics and lilac-purple flower. No specimen was mentioned in the protologue, but later, in *Flora Capensis*, Baker (1896) cited a Roxburgh collection, without number, which would be the type, although its location is unknown today. Lewis (1956), who raised the variety to species rank, reasoned that in the absence of a type specimen, the name var. *roxburghii* must apply to this local endemic of the mid Olifants River Valley, rather than *S. galeata*, which also has finely fibrous corm tunics, but flowers that, either alive or dry, are not violet-purple. Lewis's reasoning is somewhat suspect, however, because the flowers of *S. roxburghii* also do not dry this colour. We have not been able to locate the type at K, G, or CGE, where Roxburgh duplicates are sometimes located, nor at any of the many other herbaria, the collections of which we have examined. In the absence of authentic or type material, Goldblatt (1992) designated a neotype for the species to fix the application of the name as currently interpreted.

Representative specimens

WESTERN CAPE: **3218** (Clanwilliam): Algeria turning, Olifants River Valley, (–BD), 10 Sept. 1949, *Barker 5756* (NBG, SAM); 15 miles [± 23 km] N of Citrusdal, (–BD), Sept. 1942, *Lewis 1345* (SAM), Sept, 1957, *Lewis 5207* (MO, NBG); 20 miles [30 km] S of Clanwilliam, 31 Aug. 1938, *Salter 7495* (SAM); Farm Hexrivier, stony ridge adjacent to citrus orchard, (–BD), 8 Sept. 1998, *Goldblatt & Manning 11009* (MO, NBG).

12. **Sparaxis galeata** *Ker Gawl*. in Annals of Botany (König & Sims) 1: 225 (1804a), as a new name for *Gladiolus galeatus* Jacq.: 167 (1792) & : t. 258 (1794b), illegitimate homonym, not *G. galeatus* Burm.f.: 1768 (= *Gladiolus alatus* L.). *Synnotia galeata* (Ker Gawl.) Sweet: 398 (1826a). Lewis: 143 (1956). *Hebea galeata* (Ker Gawl.) Eckl.: 41 (1827). *Anactorion galeatum* Raf.: 34 (1838). Type: South Africa, [Western Cape], without precise locality or collector, illustration in Jacq.: t. 258 (1794b).

Illustration: Pole-Evans: pl. 162 (1925) [as *Synnotia bicolor*].

Plants 120–200(–350) mm high, stem branching from base or unbranched. *Corm* 16–22 mm diam., tunics of pale, fine fibres accumulating in thick mass and extending upwards to ground level in collar around stem base. *Leaves* 5–7, narrowly lanceolate, obtuse to acute, obliquely apiculate, usually inclined toward ground, ± half as long as stem, 10–18 mm wide, speckled purple on sheaths. *Spike* ± secund, 4–7-flowered, branches with fewer flowers, weakly flexuose, straight or inclined; bracts pale with dark brown streaks, becoming brown above, somewhat lacerate, outer 13–16 mm long, 3-cusped with central cusp more prominent, inner slightly shorter than outer, 2-cusped. *Flowers* zygomorphic, upper tepals violet or dull yellow-brown, lower tepals deep yellow shading to violet at tips, upper laterals fading to pale yellow distally, throat streaked purple and yellow on abaxial side, with heavy, sweet slightly spicy odour; perianth tube obliquely funnel-shaped, 12–15 mm long; tepals unequal, dorsal largest, erect, 25–30 × 14–15 mm, widest in midline, upper laterals recurved, ± 22 mm long, lower tepals united with upper lateral for ± 5 mm and to each other for ± 2 mm, free parts ± 17 × 5–6 mm, narrowly clawed at base, limbs channeled, flexed downward. *Stamens* unilateral, arcuate, filaments 18–20 mm long, translucent purple, anthers 5–6 mm before dehiscence, shrinking to ± 3 mm, pollen yellow. *Style* arched above filaments, purple, dividing opposite middle to apex of anthers, branches weakly recurved, 4–5 mm long, filiform, slightly expanded and forked at tips, ciliate on margins. *Capsules* barrel-shaped to subglobose, 5–8 mm long. *Seeds* ± 2.2 mm in diam., yellow-brown, 2 or 3(4) per locule. *Chromosome number* 2*n* = 20. *Flowering time*: early August to mid-September. Figure 18, Plate 4D.

Distribution and biology: *Sparaxis galeata* is distributed through the lower Olifants River Valley between the Nardouws Mountains and Klawer northwards along the foot of the Matsikamma–Bokkeveld Escarpment, extending through the Kobee Valley onto the southern escarpment near Lokenberg, with an isolated collection on the Hantam Plateau from the Farm Driefontein southwest of Calvinia (Figure 14). Plants occur on dry arid stony clay flats and slopes. The large, brightly coloured and strongly fragrant flowers are adapted for pollination by large, long-tongued bees, which visit the flowers to forage on the small quantity of nectar secreted in the base of the tube. Plants first sampled by Goldblatt *et al*. (2000) appeared to lack nectar, but a second population in the Kobee valley that we examined later produced ample sugary nectar (31.7% mean sucrose equivalents). At sites at the foot of Vanrhyn's Pass and in the Kobee Valley the large, long-tongued bee, *Anthophora diversipes*, has been recorded pollinating the species (Goldblatt *et al*. 2000 and unpublished). The flowers are self-incompatible and strongly protandrous. The stigmatic tips of the style branches recurve late in the flowering cycle and then come in contact with pollen, but self-pollination rarely occurs because of self-incompatibility. Seed set via deliberate or accidental selfing is very infrequent. The unusually small capsules, 5–8 mm long, contain only 2 or 3(4) seeds per locule.

Conservation status: VU (Vulnerable), but we suggest R (Rare) as the species has been recorded at several sites, all of them relatively undisturbed (Table 2).

Diagnosis and relationships: *Sparaxis galeata* is recognized by the large flowers with a particularly large, erect dorsal tepal, 20 × 12 mm, held vertically above the small, spooned and downcurved lower tepals. The flowers are usually strongly scented. The finely fibrous corm tunics accumulate in a dense mass around the corm and base of the stem, and the somewhat obtuse leaves are speckled with red to purple at the base. The capsules are unusually small for the genus, 5–8 mm long and contain at most four seeds per locule (compared with as many as 8–10 per locule in *S. villosa* and 10–12 in *S. metelerkampiae*). Based on morphology alone, we suggest that *S. galeata* is most closely allied to *S. roxburghii*, which has similar finely fibrous corm tunics that form a collar around the stem base, usually speckled leaf bases, and a prominent, erect dorsal tepal. Flowers of *S. roxburghii* are differently coloured, and have a perianth tube 20–30 mm long compared to 12–15 mm in *S. galeata*. The molecular-based phylogeny (Figure 1a, b), however, suggests that *S. roxburghii* is more closely allied to *S. auriculata*, but all three species are clearly related and share unusually small, rounded capsules with only 2–4 seeds per locule.

A population on the southern slopes of Mauwerskop near Vanrhynsdorp (*Snijman 1059*) has somewhat smaller, rather dull beige-coloured flowers, the dorsal tepal yellow-brown and only 16–20 mm long (vs. 25–30 mm in other populations), but the shape of the flower and all other features correspond with typical *G. galeata*. Flowers of this population have filaments ± 18 mm, anthers ± 6 mm, and notably a shorter style dividing opposite the middle of the anthers rather than at their apices.

FIGURE 18.—*Sparaxis galeata*, *Goldblatt & Porter 11792*. A, flowering plant; B, half-flower; C, outer (left) and inner (right) bracts; D, infructescence; E, seed. Scale bar: A, B, D, 10 mm; C, 5 mm; E, 2 mm. Artist: J.C. Manning.

History: based on living plants grown at Schönbrunn Gardens in Vienna, Austria, *Sparaxis galeata* was described in 1792 (the illustration was published two years later in 1794) by Nicholas Jacquin as *Gladiolus galeatus*. Although not recorded, the plants were probably originally collected by Franz Boos and Georg Scholl, who provided Jacquin with numerous Cape species in the years 1786 onward into the 1790s (Gunn & Codd 1981). The painting that accompanies the description in the sumptuous *Icones plantarum rariorum* leaves no doubt about the identity the plant. The name is, however, a homonym for a species described by Burman fil. in 1768, which is in turn a later synonym for *Gladiolus alatus* L., which *S. galeata* broadly resembles in flower form but not in colouration or foliage. Ker Gawler's transfer of Jacquin's name to *Sparaxis* in 1805 is to be treated as a new name with Ker Gawler as the sole authority. Robert Sweet assigned the species to his new genus *Synnotia* in 1827, an action initially followed by Baker (1878). Later, Baker (1896) included the species in *Synnotia bicolor*, and it was figured under this name in *The Flowering Plants of South Africa* (Pole-Evans 1925). Klatt (1862), who first regarded *S. galeata* as conspecific with *S. bicolor*, subsequently recognized *S. galeata*, as did Lewis (1956) in her revision of the genus.

Representative specimens

NORTHERN CAPE.—**3119** (Calvinia): Farm Driefontein, SW of Calvinia, 1 000 m, (–DA), Sept. 1921, *Marloth 10426* (PRE).

WESTERN CAPE.—**3118**: (Vanrhynsdorp) flats W of Matsikamma (DB), *Oliver 4990* (PRE); Mauwerskop, Vanrhynsdorp, (–DB), 20 Aug. 1986, *Snijman 1059* (NBG); between Klawer and Trawal, S of the Olifants River bridge (–DC), 23 Aug. 1984, *Goldblatt 7234A* (MO, PRE). **3119** (Calvinia): foot of Vanrhyns Pass (–AC), 22 Aug. 1950, *Lewis 4988* or *s.n.* (K, MO, NBG, PRE, SAM 60136), 22 Aug. 1950, *Barker 6445* (NBG, PRE), 30 Aug. 1956, *8663* (NBG); Kobee Valley, in renosterveld near stream, (–CA), 1 Sept. 2001, *Goldblatt & Porter 11792* (K, MO, NBG, PRE); Lokenburg, 335 m, (–CA), 23 Aug. 1980, *Van Berkel 197* (NBG); 7 mi. [11.2 km] SW of Klawer, Farm Driefontein, 2 mi. [3.2 km] E of Claypan [Kleipan Siding], stony koppie, (–DC), 6 Sept. 1955, *Nieuwoudt s.n.* (SAM).

13. **Sparaxis caryophyllacea** *Goldblatt* in Annals of the Missouri Botanical Garden 79: 156 (1992). Type: [Western Cape], middle slopes of the Nardouw Mtns, north of Clanwilliam, 13 Aug. 1976, *Goldblatt 3851* (NBG!, holo.; K!, MO!, PRE! iso.).

Plants 120–300 mm high, often with 1 or 2 branches produced in axils of cauline leaves. *Corm* 13–18 mm diam., tunics of hard, coarse, vertical fibres, often thickened below into claw-like ribs. *Leaves* 5–7, mostly basal, upper 1 or 2 cauline, inserted in mid part of stem, broadly oblanceolate, reaching to about middle of stem, 10–15 mm wide, usually obtuse, apiculate, sometimes obliquely so, lower leaves usually speckled with red to purple (fading on drying), often inclined (leaves of juvenile plants usually ± prostrate). *Spike* straight or barely flexuose, 2–4-flowered, ± secund, lateral spikes when present with fewer flowers; bracts pale below with whitish veins, becoming light brown above, outer 12–14 mm long, lacerate, with prominent central cusp, inner 2-cusped. *Flowers* zygomorphic, pale yellow with dorsal tepal shading to violet in distal half, upper lateral tepals cream above base, lower tepals deep yellow, fading to cream at tips, throat yellow with prominent dark streaks, sweetly carnation-scented; perianth tube funnel-shaped, curving outward distally, ± 20 mm long; tepals unequal, dorsal erect to slightly hooded, 24–28 × 12–14 mm, upper laterals ± 16 × 8–9 mm, directed forward, lower tepals united for 3 mm, ± horizontal proximally, ± 12 × 6–7 mm, flexed downwards and channelled distally. *Stamens* unilateral and arcuate; filaments ± 12 mm long, whitish; anthers ± 4.5 mm long, white, only partially exserted from mouth of tube; pollen ± white. *Ovary* ± 3.5 mm long, ovoid-trigonous, style arched over filaments, white, dividing shortly below anther apices, branches ± 6 mm long, diverging, recurved in distal half, spreading beyond anthers, conduplicate below, becoming narrowly channeled towards upper third and margins sparsely ciliate. *Capsule* broadly ovoid, 10–11 × 6–7 mm; *seeds* globose, glossy brown, 1.8–2.2 mm diam., usually 10 per locule. *Chromosome number* $2n = 20$. *Flowering time*: August. Figure 19, Plate 5A.

Distribution and biology: a very local endemic, *Sparaxis caryophyllacea* is known only from the western slopes at the northern end of the Nardouw Mountains along the Olifants River Valley, between Bulshoek and the confluence of the Doorn River north of Trawal (Figure 20). It was evidently first collected in 1976, remarkably late for a fairly conspicuous plant. *S. caryophyllacea*

FIGURE 19.—*Sparaxis caryophyllacea*, *Goldblatt, Manning & Porter 112854A*. A, flowering plant; B, half-flower; C, outer (left) and inner (right) bracts; D, infructescence; E, seed. Scale bar: A, B, D, 10 mm; C, 5 mm; E, 2 mm. Artist: J.C. Manning.

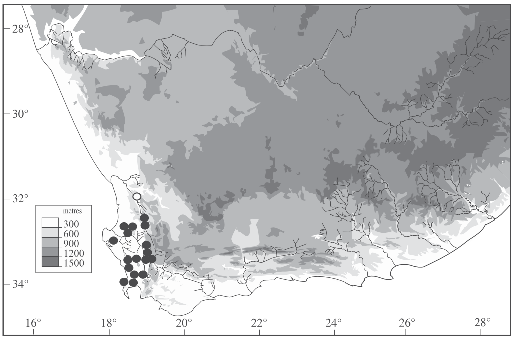


FIGURE 20.—Distribution of *Sparaxis villosa*, ●; *S. caryophyllacea*, ○.

grows in stony clay, below the contact line with the lowermost band of Table Mountain Sandstone that caps the Nardouw range. The relatively large flowers are sweetly scented.

Sparaxis caryophyllacea is self-compatible and sets full capsules, containing ± 30 seeds, when hand pollinated with its own pollen and is sometimes autogamous in the greenhouse. In nature the species is most likely normally outcrossing, and is pollinated by large-bodied anthophorine bees, *Anthophora* spp. (Goldblatt *et al*. 2000).

Conservation status: CR (Critically Rare). The only known population, though small, is most likely more extensive than known at present. Although under no immediate threat, future widening of the road will be detrimental.

Diagnosis and relationships: the flowers resemble most closely those of *Sparaxis villosa* (Figure 21), but the similarity may be because this is the ancestral flower type in the genus rather than an indication of close relationship. *S. caryophyllacea* can be distinguished by the relatively large flower size alone, the dorsal tepal 24–28 mm long compared with 12–16 mm in *S. villosa*. In addition the pale yellow perianth is conspicuously striped with black in the throat and strongly carnation scented. Another diagnostic feature is the red to purple speckling on the sheaths of the lower leaves. This character is also present in *S. galeata*, presumably due to convergence, for the two do not seem immediately related.

In the molecular phylogeny (Figure 1b) based on a combined analysis of plastid and nuclear DNA sequences, *Sparaxis caryophyllacea* is retrieved as sister to the *S. tricolor* clade (but with weak statistical support) and together with these three species comprises a clade sister to the remaining species of *Sparaxis*. We see no morphological features in support of this association. We also note that in the nuclear gene-based phylogeny (Figure 1a), *S. caryophyllacea* is retrieved in an entirely different position, as sister to a clade including *S. villosa* plus the two long-tubed species, *S. metelerkampiae* and *S. variegata* (BP 80). This clade shares one notable synapomorphy, coarsely fibrous corm tunics. In light of the nuclear gene-based phylogeny and the shared coarsely fibrous corm tunics we treat *S. caryphyllacea* as allied to the *S. villosa/variegata* species group.

Sparaxis caryophyllacea would make a fine container or rock garden subject. It is as easy to grow as *S. tricolor* and the *Sparaxis* hybrids available in the horticultural trade. In years of ample rainfall in its native habitat, plants make a fairly impressive display on the rocky slopes.

Representive specimens

WESTERN CAPE.—**3118** (Vanrhynsdorp): Nardouw Mtns, upper third of Brand-se-Berg Pass, (–DA), 2 Sept. 1981, *Goldblatt 6162* (MO), 23 Aug. 2007, *Goldblatt, Manning & Porter 112854A* (MO, NBG).

14. **Sparaxis villosa** *(Burm.f.) Goldblatt* in Annals of the Missouri Botanical Garden 79: 156 (1992). *Gladiolus villosus* Burm.f.: 2 (1768). *Synnotia villosa* (Burm.f.) N.E.Br.: 133 (1929). Lewis: 142 (1956). Type: South Africa, [Western Cape], without precise locality, illustration in Breyne: t. 8, f. 2 (1739) [lecto., effectively designated by Brown: 133 (1929)].

Gladiolus bicolor Thunb.: no. 16, t. 2, f. 1 (1784). *Ixia bicolor* (Thunb.) Ker Gawl.: t. 548 (1802). *Sparaxis bicolor* (Thunb.) Ker Gawl.: 225 (1804a). *Synnotia bicolor* (Thunb.) Sweet: 398 (1826b). Baker: 134 (1896), excl. syn. *Gladiolus galeatus* and var. *roxburghii*. *Hebea bicolor* (Thunb.) Eckl.: 42 (1827). *Anactorion bicolor* (Thunb.) Raf.: 34 (1838). Type: [Western Cape], Groene Kloof, *Thunberg s.n.* (UPS–Herb. Thunberg, syn.! [two sheets]).

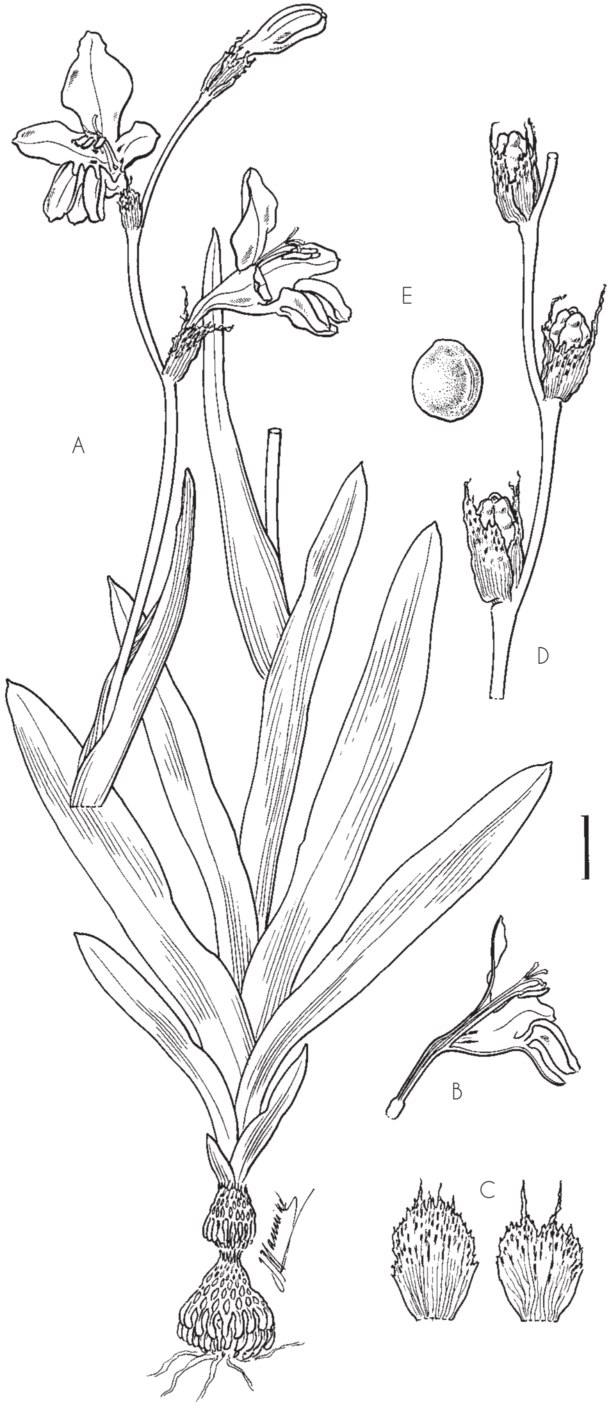


FIGURE 21.—*Sparaxis villosa*, *Goldblatt 6125*. A, flowering plant; B, half-flower; C, outer (left) and inner (right) bracts; D, infructescence; E, seed. Scale bar: A, B, D, 10 mm; C, 5 mm; E, 2 mm. Artist: J.C. Manning.

Illustrations: Manning & Goldblatt: 66 (1996); Manning *et al*.: 360 (2002).

Plants 150–350 mm high, stem simple or with 1 branch produced in axil of cauline leaf. *Corm* 9–15 mm in diam., tunics of hard, coarse fibres, netted above, thickened and vertical below, often forming claw-like ridges. *Leaves* 5–7, mostly in a basal fan, uppermost inserted in middle of stem, narrowly lanceolate, obliquely apiculate, reaching to between middle of stem and base of spike, 5–15 mm wide, sheathing lower part of stem. *Spike* weakly flexuose, subsecund, 2–4-flowered; bracts pale below with whitish veins, becoming irregularly streaked light brown above, outer 15–25 mm long, ± 3 cuspidate with central cusp prominent, becoming irregularly lacerate, inner ± as long as outer, with 2 prominent cusps. *Flowers* zygomorphic, creamy yellow with dorsal tepal violet in upper half and lower tepals deep yellow fading to cream at tips, abaxial half of throat streaked yellow and violet, unscented; perianth tube obliquely funnel-shaped, upper part curving outward, (12–)15–16 mm long; tepals unequal, dorsal largest, erect to slightly hooded, (10)15–16 × 9–10 mm, upper laterals ± 12 mm long, directed forwards, lower three tepals united basally for ± 2 mm, ± horizontal below, ± 10 mm long, channelled and flexed downward distally. *Stamens* unilateral, arcuate, filaments ± 13 mm long, white, anthers violet above, cream below, ± 3 mm long, fully exserted, pollen ± white. *Ovary* 4–5 mm long, oblong-trigonous, style arched over filaments, purple, dividing just below or opposite anther bases, branches ± 2 mm long, ascending, recurved distally, ciliate along margins ± to base, slightly expanded distally. *Capsules* barrel-shaped, ± 12 × 6–7 mm. *Seeds* 1.7–2.1 mm diam., light brown, (8)9 or 10 per locule. *Chromosome number* $2n = 20$. *Flowering time*: mid-August to late September. Figure 21, Plate 5B.

Distribution and biology: the most widespread species of sect. *Sparaxis*, *S. villosa* extends from the Cape Peninsula northward along the west coast and through the Tulbagh and Olifants River Valleys as far north as the Piketberg and Citrusdal (Figure 20). It occurs in renosterveld on heavy clay and granite derived soils, often in rocky sites but also under low shrubs where it blooms more erratically than in open habitats. The modest-sized and fairly inconspicuous flowers appear likely to be insect pollinated but the species is self-compatible. Plants from two populations have proven to be autogamous when grown in the greenhouse and isolated from potential pollinators. The stigmas are receptive as soon as the anthers shed their pollen and the style branches remain in contact with the anthers throughout anthesis, ensuring contact of pollen with the stigmatic surfaces from the time the pollen is released. Selfing results in the production of full capsules with (8)9 or 10 seeds per locule (typically 27–30 seeds per capsule), the normal complement for the species. The autogamous habit may account for the comparatively wide range of *S. villosa*.

Sparaxis villosa hybridizes with *S. metelerkampiae* at the foot of Piekeniers Kloof Pass (*Goldblatt, Manning & Porter 13480* MO, NBG). Although mostly separated geographically and edaphically, the ranges of the two species overlap for a short distance and at this locality they co-occur on loamy soils at the shale-sandstone interface.

The species is naturalized in the Mt. Lofty Range of South Australia (Cooke 1986; *Eichler 18696* NBG).

Conservation status: LC (Least Concern).

Diagnosis and relationships: *Sparaxis villosa* is most easily recognized by its comparatively small flower with an erect to slightly hooded, dorsal tepal usually ± 16 mm long, much exceeding the yellow lower tepals, ± 10 mm long. The distinctive coarse corm tunic fibres are also shared with the rare *S. caryophyllacea*, which has larger flowers, the dorsal tepal ± 20 mm long. The two long-tubed species, *S. metelerkampiae* and *S. variegata*, also have similar corm tunics but the long perianth tube immediately sets them apart. These distinctive corm tunics define the lineage comprising these four species. The small-flowered form of *S. villosa* with tunics of fine fibres mentioned by Goldblatt (1992) from the Saldanha district is now recognized to represent a separate species, *S. calcicola*. A particularly small-flowered variant of *S. villosa* (*Lewis 5979* NBG) has been recorded on granite outcrops at Vredenburg, with a dorsal tepal ± 10 mm long and perianth tube ± 12 mm long. These plants might easily be misidentified as *S. parviflora* were it not for the distinctive coarsely fibrous tunics.

History: when first described in 1768 by N.L. Burman, *Sparaxis villosa* was referred to *Gladiolus*. Burman based *G. villosus* on an illustration published in Jacob Breyne's (1739) volume, *Prodromi fasciculi rariorum plantarum*, a series of illustrations of rare, cultivated plants. The specific epithet *villosus* refers to the deceptively hairy appearance of the long-cuspidate and sometimes torn floral bracts. A satisfactory identification of Burman's *G. villosus* was made only in 1929 when N.E. Brown systematically reviewed and typified the Cape Iridaceae described by N.L. Burman in 1768. Prior to this time, *S. villosa* was known as *Synnotia bicolor* (Sweet 1826b; Baker 1896); a species based on *Gladiolus bicolor*, described by C.P. Thunberg in 1784 and collected by him at the Cape, some 10 years earlier.

Representative specimens

WESTERN CAPE.—**3217** (Vredenburg): hill above Saldanha Bay, (–DD), 7 Aug. 1966, *Pamphlett 67* (NBG); Vredenburg, granite rocks, 6 Aug. 1962, *Lewis 5979* (NBG). **3218** (Clanwilliam): Moutonsvlei, W of Piketberg, sand, (–DA), 21 Aug. 1984, *Goldblatt 7194* (E, MO, PRE, WAG); flats N of Piketberg, foot of Zebrakop, renosterveld, (–DB), 1 Sept. 1981, *Goldblatt 6125* (K, MO, NBG, WAG); Piketberg, Kapteins Kloof, northern end, renosterveld, (–DC), 20 Sept. 1974, *Goldblatt 2722* (MO). **3219** (Wuppertal): rocky sandstone slope N of Citrusdal (–CA), 1 Sept. 1981, *Goldblatt 6147* (MO). **3318** (Cape Town): Darling, (–AC), 23 Aug. 1947, *Compton 19880* (NBG); Malmesbury commonage, (–BC), *Lewis 3558* or *s.n.* (PRE, SAM); Malmesbury, 12 Sept. 1947, *Barker 4667* (NBG), 21 Aug. 1950, *6394* (NBG); clay slopes, Signal Hill, (–CD), *Marloth 188* (PRE); Lions Mt., (–CD), *MacOwan 798* (BOL, G, GH, K); between Salt River and Kalabas Kraal (–DA), *Hutchinson 175* (K, PRE); Langverwacht above Kuils River, (–DC), 26 Sept. 1973, *Oliver 4657* (K, MO, PRE); Wellington, (–DD), 21 Aug., *Martin 1052* (NBG); Dal Josephat, (–DD), 25 Aug. 1926, *Grant 2333* (MO); foot of Paarl Mountain, (–DD), in 1838, *Harvey s.n.* (CGE, TCD). **3319** (Worcester): Saron (–AA), 18 Aug. 1894, *Schlechter 4869* (BOL, C, G, K, PRE, SAM, Z); Tulbagh Kloof, (–AC), *Ecklon & Zeyher Irid. 121* (77.9) (E, G, GH, MO, SAM); fields near Tulbagh, 400 ft [122 m], (–AC), 3 Sept. 1892, *Schlechter 1416* (Z); foot of Michell's Pass, 9 miles [13.5 km] from Ceres, (–AD), *Goldblatt 220* (BOL); lower slopes of the Witzenberg, N of Michell's Pass, (–AD), 8 Sept. 1976, *Goldblatt 4076* (MO).

15. **Sparaxis variegata** *(Sweet) Goldblatt* in Annals of the Missouri Botanical Garden 79: 157 (1992). *Synnotia variegata* Sweet: t. 150 (1826b). Baker: 135 (1896). Lewis: 147 (1956), in part excluding var. *metelerkampiae*. Type: South Africa, without precise locality or collector, illustration in Sweet: t. 150 (1826a).

Sparaxis wattii Harvey: 330 (1838). Type: South Africa, [Western Cape], without precise locality, *Watt s.n.* (TCD, holo.!; GH, K!, iso.).

Plants 100–180(–300) mm high, stem simple or sometimes branched near middle. *Corm* 12–22 mm diam., tunics of coarse, hard fibres, with thickened vertical strands in lower half. *Leaves* several in a tight fan, inclined or appressed to ground, 100–150 × 8–14 mm. *Spike* secund in two ranks, 3–8-flowered, branches always with fewer flowers than main spike; bracts pale with brown streaks, margins irregularly toothed, outer 20–25 mm long, inner ± as long, divided distally into 2 long cusps. *Flowers* zygomorphic, bilabiate, either pale yellow with dorsal tepal violet and lower laterals purple at tips or less often upper three tepals violet, throat yellow to white with longitudinal purple streaks, unscented; perianth tube cylindric below, abruptly bent at right angles into wide horizontal part, cylindrical part 30–32 mm long, ± 2 mm diam., upper part ± 12 mm long, slightly inflated, ± 12 mm wide at mouth; tepals unequal, dorsal longest, ± erect, lanceolate-ovate, 25–30 × 16–18 mm, upper laterals ± 20 × 10 mm, recurving in distal half, lower tepals united basally for 5–7 mm, ± clawed, limbs channeled, ± 12 × 4.5 mm. *Stamens* unilateral and arcuate, filaments ± 20 mm long, anthers parallel, white, striped purple on locule sutures, 6–7 mm long. *Ovary* ovoid, ± 3 mm long, style dividing near anther tips, branches recurving gradually, 4–5 mm long, channelled and broader in distal half with ciliate margins, apex emarginate. *Capsules* oblong, 9.0–11.5 × ± 6 mm. *Seeds* globose, brown, ± 2 mm diam., (5–)8–9(10) per locule. *Flowering time*: late August to mid-September. Figure 22, Plate 5C.

Distribution and biology: centred in the lower Olifants River valley between Clanwilliam and Bulshoek, *Sparaxis variegata* occurs on rocky sandstone slopes, sometimes along the courses of temporary streams, often on south-trending slopes (Figure 23). Both it and related *S. metelerkampiae* are pollinated by the long-proboscid fly, *Prosoeca peringueyi*, which visit the flowers for nectar. Although we initially reported that *S. variegata* was pollinated by large, long-tongued *Anthophora* bees (Goldblatt *et al*. 2000), based on occasional

FIGURE 22.—*Sparaxis variegata*, *Goldblatt & Manning 10720C*. A, flowering plant; B, half-flower; C, outer (left) and inner (right) bracts; D, infructescence and detached capsule; E, seed. Scale bar: A, B, D, 10 mm; C, 5 mm; E, 2 mm. Artist: J.C. Manning.

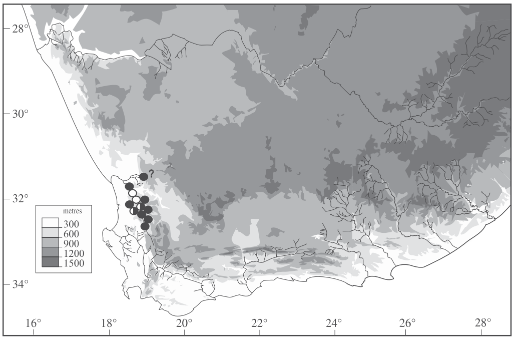


FIGURE 23.—Distribution of *Sparaxis variegata*, ●; *S. metelerkampiae*, ○.

visits by this bee to its flowers, our later observations contradict this. The bees cannot reach nectar in the lower part of the tube and visits we have recorded are either merely exploratory or part of a bimodal pollination system utilising both bees and flies, as has been recorded in *Tritoniopsis toximontana* (Manning & Goldblatt 2005). We have noted and captured *Prosoeca peringueyi* visiting *S. variegata* in Nardouw Kloof where their activity was constant, flies moving from one flower to the next, eventually taking nectar from all the open flowers in the population. Laboratory studies have shown that *S. variegata* is self-incompatible and it thus depends for its pollination for the most part by a single species of long-proboscid fly.

Conservations status: LC (Least Concern), but we recommend VU (Vulnerable), because of its rarity and narrow range.

Diagnosis and relationships: the large flowers of *Sparaxis variegata* are either yellow with the dorsal tepal pale violet or predominantly violet with the lower tepals either yellow or white tipped with violet and the throat white streaked with purple lines. The types of both *S. variegata* and the synonym *S. wattii* correspond to the violet-flowered form, which is less common and occurs in the south of the range, notably at Rondegat, south of Clanwilliam. The larger size of the flowers including the tepals and anthers, a style that divides near the anther apices, and often the predominantly yellow perianth distinguish *S. variegata* from closely allied *S. metelerkampiae*. The longer style with the branches arched above the anthers makes self-pollination unlikely, but in any event, the species is genetically self-incompatible. The capsules, up to 11 mm long, typically contain 8–10 seeds per locule. Like its close relative *S. metelerkampiae*, *S. variegata* has corms with coarsely fibrous tunics and flowers with a long perianth tube with a strong geniculate bend at the apex of the slender, cylindric part of the tube.

We suspect that some interbreeding and introgression occurs with *Sparaxis metelerkampiae* in the large population of *S. variegata* that occurs on south-trending slopes near Rondegat, south of Clanwilliam. Flower size is unusually variable at this locality and the predominantly purple colouration may be derived through hybridization with *S. metelerkampiae*, which grows nearby (see Natural hybrids).

History: *Sparaxis variegata* was first described as *Synnotia variegata* by Robert Sweet in 1826 based on plants grown in England. His plants were probably raised from seeds or corms sent by Walter Synnot, landdrost (magistrate) at Clanwilliam from 1821 to 1825. The species is also the type of the genus *Synnotia*, described by Sweet at the same time and named in honour of Synnot. Lewis (1956) treated *S. variegata* as including *S. metelerkampiae* at varietal rank. In 1992, *Synnotia* was reduced to synonymy in *Sparaxis* and at the same time var. *metelerkampiae* was raised to subspecies rank in *S. variegata* (Goldblatt 1992). *S. metelerkampiae* was accorded species rank in *Sparaxis* by us in 1999 (Goldblatt & J.C.Manning 1999).

Representative specimens

WESTERN CAPE.—**3118** (Vanrhynsdorp): between Klawer and Clanwilliam, road verge, (–DA), 23 Aug. 1984, *Goldblatt 7235* (MO); Nardouw road at top of pass (–DC), 6 Sept. 1951, *Barker 7435* (NBG), 15 Sept. 2002, *Goldblatt & Porter 12211* (MO, NBG); Nardouw Pass, (–DC), *Lewis 1874* (SAM); near Olifants River Barrage (–DD), 23 Aug. 1941, *Barker 1477* (NBG), *Esterhuysen 5809* (BOL, K, PRE), 2 Sept. 1997, *Goldblatt & Manning 10720C* (MO); 2 miles [3 km] S of Bulshoek dam, stony hill slopes, (–DD), 25 Aug. 1962, *Nordenstam 1009* (MO, S). **3218** (Clanwilliam): Rietvleiberg, Clanwilliam district, (–BA), 3 Sept. 1072, *Oliver 3827* (K, NBG); banks of the Olifants river near Rondegat, (–BD), 26 Aug. 1894, *Schlechter 5037* (partly) (BOL, COI, G, K, P, PRE, Z).

16. **Sparaxis metelerkampiae** *(L.Bolus) Goldblatt & J.C.Manning* in Bothalia 29: 61 (1999). *Synnotia metelerkampiae* L.Bolus: 77 (1923). *Sparaxis variegata* var. *metelerkampaie* (L.Bolus) G.J.Lewis: 148 (1956). *Sparaxis variegata* subsp. *metelerkampiae* (L.Bolus) Goldblatt: 158 (1992). Type: South Africa, [Western Cape], Eendekuil, *Metelerkamp s.n.* (BOL16039, holo.!; K!, PRE! iso.).

Sparaxis orchidiflora Lodd.: t. 1099 (1826), nom. nud.

Sparaxis luteoviolacea Ecklon: 27 (1827) nom. nud. (based on *Ecklon & Zeyher 76.8*: C, E, G, GH, P).

Illustrations: Pole-Evans: pl. 98 (1923) [as *Synnotia variegata*]; Manning & Goldblatt: 83 (1997) [as *Sparaxis variegata*]; Manning *et al.*: 359 (2002).

Plants 120–300 mm high, stem simple or 1(2)-branched, inclined above leaf sheaths. *Corm* 10–16 mm diam., tunics of coarse netted fibres usually thickened below into claw-like ridges. *Leaves* 5–7, lanceolate, obtuse to acute, apiculate, sometimes obliquely so, basal except uppermost, this inserted in middle of stem, ± 1/2 to 2/3 as long as stem, 7–12 mm wide, sheathing lower part of stem, often inclined toward ground. *Spike* ± secund, 2–5-flowered; bracts pale or irregularly streaked with brown, slightly crinkled, outer 15–18 mm long, 3-cuspidate, central cusp more prominent, inner slightly shorter, with 2 prominent cusps. *Flower* violet-purple with cream to yellow (rarely reddish) markings on lower tepals; perianth tube with cylindric lower part 35–40 mm long, upper part 10 mm long, 6–7 mm wide at mouth; tepals unequal, dorsal largest and erect with margins incurved, 15–20 mm long, 8–11 mm wide, upper laterals 12 mm long, ± 5 mm wide, directed forward below and outward in distal half, lower tepals united with upper lateral for ± 3 mm and to each another for ± 4 mm, limbs channeled below and flexed downward in distal half, ± 12 × 4–5 mm. *Stamens* unilateral, arcuate, filaments 10–12 mm long, purple, reaching top of tube or exserted up to 3 mm, anthers 3–4 mm long, purple, median anther extending beyond tips of laterals, pollen pale yellow. *Style* usually dividing opposite lower 1/3 of anthers or below them (possible hybrids have style dividing opposite or beyond anther tips), purple, branches diverging, 2–3 mm long, extending between anther bases. *Capsule* cylindric-trilobed, 12–15 mm long, 5 mm wide. *Seeds* glossy brown, globose, 1.3–1.6 mm diam., 10–12 per locule. *Chromosome number* $2n = 20$. *Flowering time*: August to mid-September. Figure 24, Plate 5D.

Distribution and biology: relatively widely distributed through the northern part of Western Cape, *Sparaxis metelerkampiae* extends from the Gifberg in the north, through the Olifants River Valley and adjacent mountains to Piekeniers Kloof and Eendekuil in the south and to Leipoldtville in the west (Figure 23). An early record from Oorlogskloof on the southern Bokkeveld Mountains (*Leipoldt 3872*) requires confirmation. It grows in sandy and stony ground, always in well drained situations. Greenhouse studies have shown that the species is fully self-compatible and autogamous. Flowers consistently set full capsules with 10–12 seeds per locule without hand pollination and in the absence of insect visitors. The flowers are, however, adapted for pollination by the long-proboscid fly *Prosoeca peringueyi* and plants often receive visits from these flies (Manning & Goldblatt 1996).

The species appears to hybridize with *S. variegata* south of Clanwilliam, and we have recorded hybrids with *S. villosa* at the foot of Piekeniers Kloof Pass (*Goldblatt, Manning & Porter 13480* MO, NBG) (see Natural hybrids).

Conservation status: LC (Least Concern). We note, however, that its range is somewhat reduced by expanding agriculture, especially rooibos tea planting. A status of VU (Vulnerable) may be more appropriate given changing conditions.

Diagnosis and relationships: *Sparaxis metelerkampiae* has long-tubed, purple flowers with the lower tepals each with a white longitudinal streak, at the center of which is a pale yellow or reddish mark. The tepals are smaller than those of immediately related *S. variegata*, the dorsal tepal 15–20 mm long vs. 25–30 in *S. variegata*, and the style is short, dividing below or opposite the lower third of the anthers and has branches 2–3 mm long, whereas in *S. variegata* the longer style divides close to the anthers' tips and the branches are 4–5 mm long. The shorter style of *S. metelerkampiae* results in the style branches and anthers coming into contact during anthe-

FIGURE 24.—*Sparaxis metelerkampiae*, Piekenierskloof Pass, without voucher. A, flowering plant; B, half-flower; C, outer (left) and inner (right) bracts; D, infructescence and detached capsule; E, seed. Scale bar: A, B, D, 10 mm; C, 5 mm; E, 2 mm. Artist: J.C. Manning.

sis, ensuring self-pollination if insect-mediated pollen transfer fails. Lewis (1956) preferred not to recognize *S. metelerkampiae*, maintaining that there are some intermediates between it and *S. variegata*, but our studies have shown that the two are usually easy to distinguish and have quite different compatibility relations. Some of the variation in perianth size in *S. variegata* may be due to growing conditions and possibly to hybridization locally, as both have the same pollinator (see Natural hybrids).

History: *Sparaxis metelerkampiae* was described by H.M.L. Bolus in 1923 in the genus *Synnotia*, based on plants from Eendekuil, a short distance south of Piekeniers Kloof Pass. It had, however, been discovered at least as early as 1827 when it was listed by Ecklon (1827) as *S. luteoviolacea* without description and thus invalid (Nordenstam 1972). Ecklon's plant was generally considered synonymous with *S. variegata* for many years. G.J. Lewis treated *S. metelerkampiae* as var. *metelerkampiae* of *S. variegata*, believing that the two intergraded over their range.

Representative specimens

WESTERN CAPE.—**3118** (Vanrhynsdorp): Zyferfontein, NE of Rietvleiberg, (–DC), 3 Sept. 1972, *Oliver 3812* (K, PRE). **3218** (Clanwilliam): Spioenkop near Leipoldtville, (–AB), 4 Sept. 1981, *Loubser 2402* (NBG); Graafwater, (–BA), 7 Sept. 1953, *Compton 24220* (NBG); between Clanwilliam and Graafwater, (–BA, –BB), *Van Breda 1267* (PRE, Z); near Paleisheuwel, (– BC), *Levyns 10154* (BOL); Farm Klein Remhoogte, W of Algeria, stony bank in sand, (–BD), 3 Sept. 1985, *Snijman 887* (MO, NBG); Algeria road 2 km E of Olifants River bridge, (–BD), 3 Sept. 1991, *Goldblatt 9147* (MO); 10 km S of Clanwilliam, 4 Sept. 1955, *Lewis 4284* (K, PRE, SAM); N of Citrusdal, Farm Hexrivier, sandstone slope, 1 Sept. 1981, *Goldblatt 6148* (MO); Grey's Pass [Piekenierskloof Pass], (–DB), 29 Aug. 1941, *Barker 1476* (NBG), *Salter 2733* (K). **3219** (Wuppertal): top of Pakhuis Pass, recently burned slopes in sandy soil (–AA), 27 Sept. 1981, *Goldblatt 6404* (MO); Pakhuis Pass, *Salter 3641* (BOL, K), *Gillett 4062* (BOL, PRE); Algeria campsite, 700 m, (–AC), 30 Aug. 1963, *Bos 503* (PRE); Elandskloof, (–CA), Sept. 1945, *Lewis 1341* (SAM); slopes behind Warm Baths, (–CA), *Stephens 7086* (BOL, K).

Unconfirmed locality: NORTHERN CAPE.—**3119** (Calvinia): Nieuwoudtville-Oorlogskloof (–AC), *Leipoldt 3872* (BOL, K).

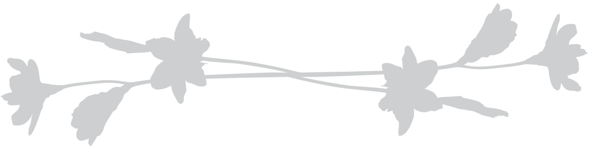


PLATE 1.—A, *Sparaxis tricolor*, Nieuwoudtville; B, *S. pillansii*, Nieuwoudtville; C, *S. elegans* salmon pink colour form, Nieuwoudtville; D, *S. elegans* white colour form, Nieuwoudtville, Farm Matjiesfontein.

PLATE 2.—A, *Sparaxis calcicola*, Jacobsbaai; B, *S. parviflora*, Darling; C, *S. grandiflora* subsp. *fimbriata*, Hermon; D, *S. grandiflora* subsp. *grandiflora*, Tulbagh.

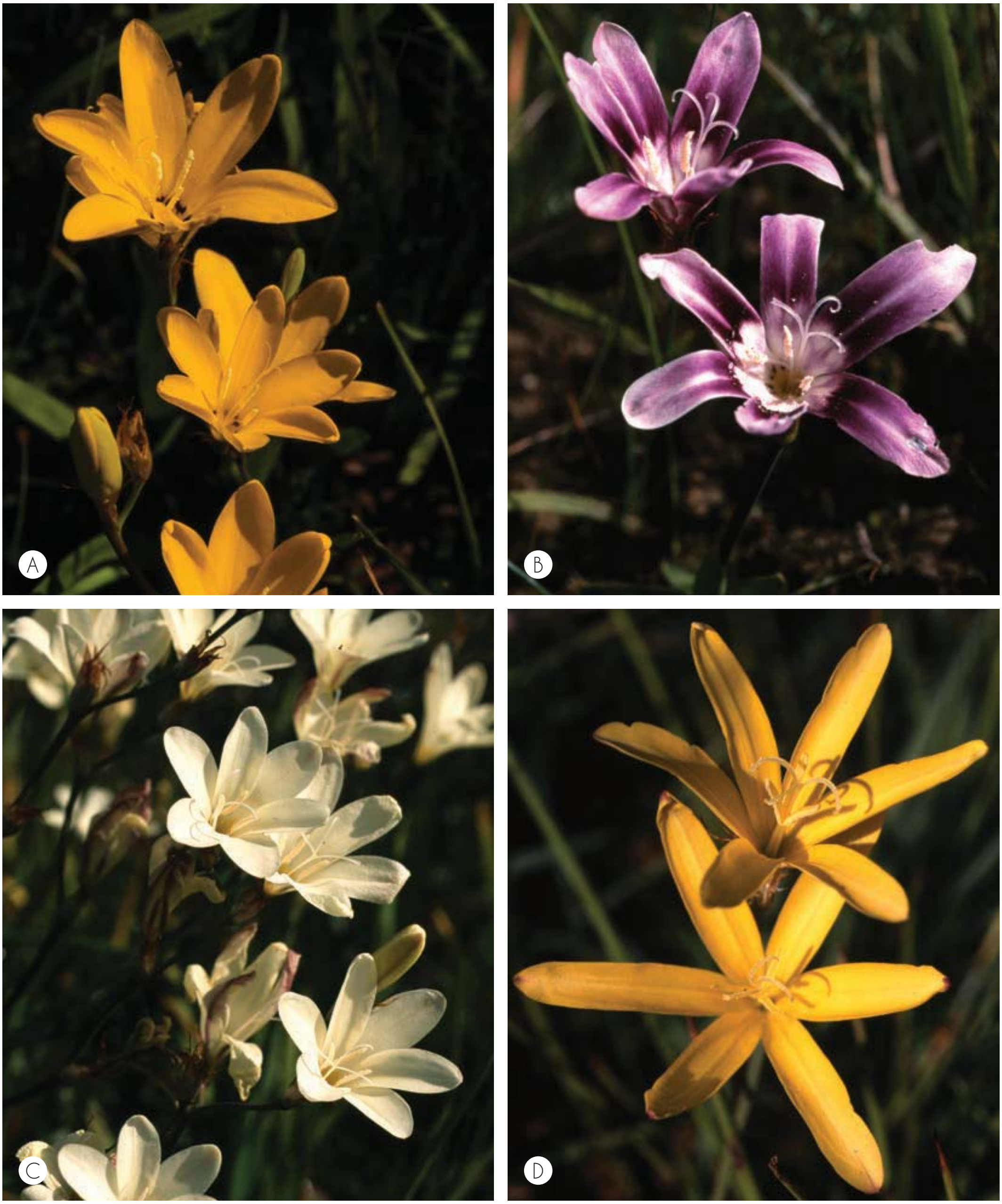


PLATE 3.—A, *Sparaxis grandiflora* subsp. *acutiloba*, Citrusdal; B, *S. grandiflora* subsp. *violacea*, Caledon; C, *S. bulbifera*, Darling; D, *S. fragrans*, Villiersdorp.

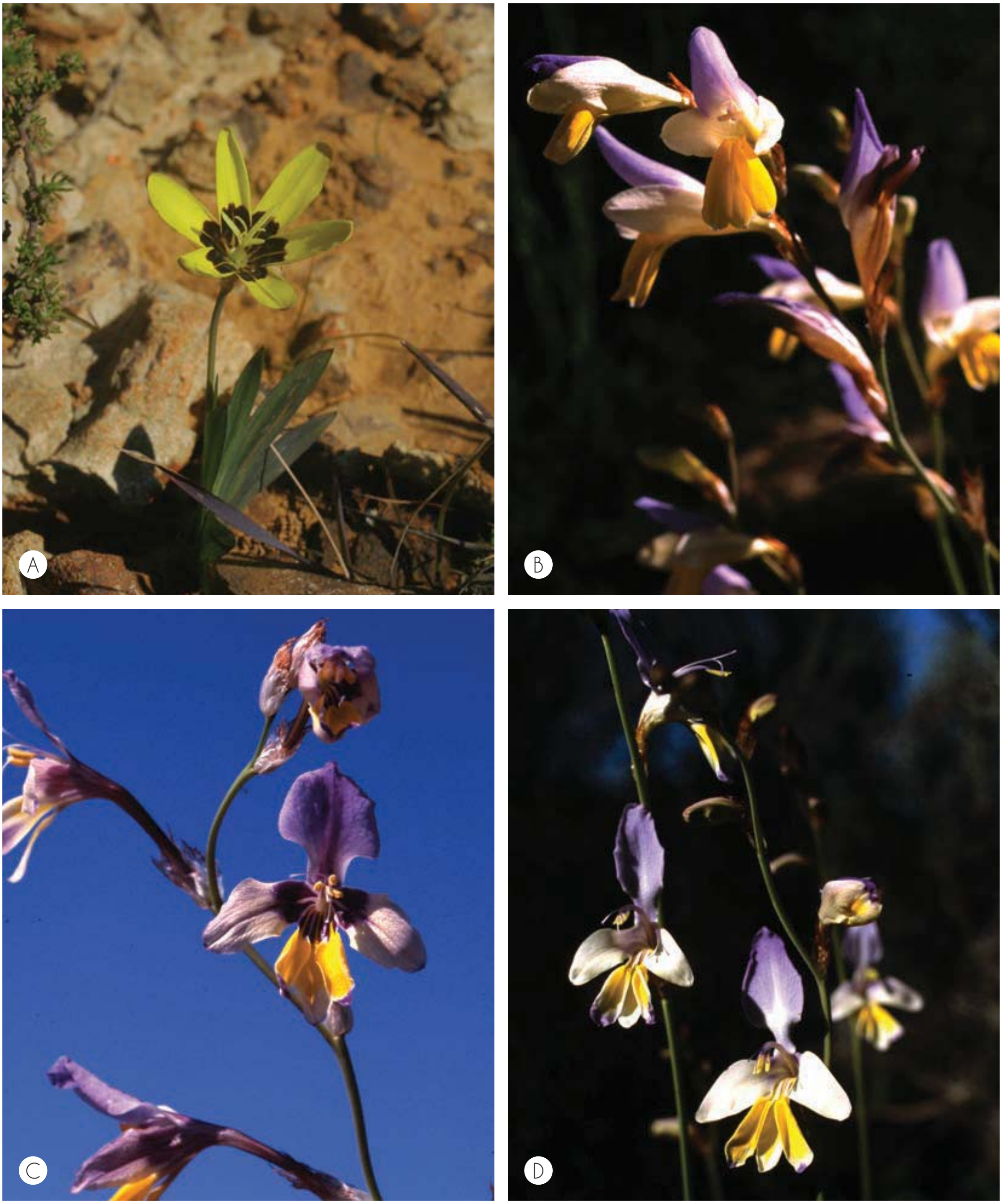


PLATE 4.—A, *Sparaxis maculosa*, Stettyn; B, *S. auriculata*, Gifberg; C, *S. roxburghii*, Citrusdal; D, *S. galeata*, Kobee.

PLATE 5.—A, *Sparaxis caryophyllacea*, Nardouw; B, *S. villosa*, Wellington; C, *S. variegata*, Trawal; D, *S. metelerkampiae*, Citrusdal.

Natural hybrids

S. bulbifera × **S. grandiflora** subsp. **fimbriata**: WESTERN CAPE.—**3318** (Cape Town): Tygerberg Nature Reserve, (–BC), without date, *Loubser 3057* (MO).

S. metelerkampiae × **S. variegata**: WESTERN CAPE.—**3218** (Clanwilliam): 22 mi. [35 km] N of Citrusdal, (–BD), 5 Sept. 1950, *Lewis 6602* (NBG).

S. metelerkampiae × **S. villosa**: WESTERN CAPE.—**3218** (Clanwilliam): foot of Piekeniers kloof Pass, (–DB), 25 Aug. 2009, *Goldblatt, Manning & Porter 13480* (MO, NBG).

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We thank Lendon Porter and Elizabeth Parker for their assistance and companionship in the field; Roy Gereau for advice with various nomenclatural questions; and Mary Stiffler who cheerfully helped solve bibliographic questions and provided copies of numerous articles not readily available to us. Collecting permits were provided by the Nature Conservation authorities of Northern Cape and Western Cape Provinces, South Africa. We are grateful to Vincent Savolainen and his laboratory group at Imperial College, London for allowing us to use unpublished molecular data on the genus, and especially Cuong Tang and Paul Rymer, now Royal Botanic Gardens, Sydney, Australia.

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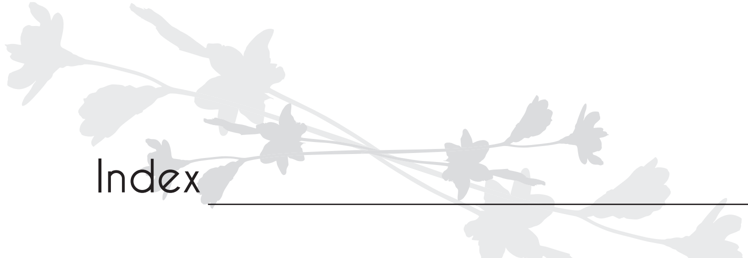

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The South African genus *Sparaxis* Ker Gawl., a member of tribe Ixieae of subfamily Crocoideae of the Iridaceae, is endemic to the western half of the winter rainfall zone of southern Africa. The genus, described by John Ker Gawler in 1802 for species until then referred in *Ixia* L. or *Gladiolus* L., includes 16 species in this monographic account. One of them from lime-enriched habitats near Saldanha Bay, *S. calcicola*, is new to science. All species are corm-bearing, seasonal geophytes with horticultural potential, and one species, *S. tricolor*, is widely available in the horticultural trade. Molecular systematic study using nuclear and plastid DNA loci confirms morphological study that the genus *Synnotia* Sweet is nested in *Sparaxis* and provides the basis for an infrageneric classification subdividing the genus into two sections. The molecular phylogeny is largely consistent with relationships inferred from morphology and shows that radial symmetry of the perianth probably evolved at least twice from ancestors with bilaterally symmetric (zygomorphic) flowers. These shifts in floral symmetry are pollinator-driven and are correlated with shifts from ancestral pollination by large-bodied anthophorine bees to either generalist pollination by multiple pollinator groups or to pollination dominated by hopliine beetles. Based on relationships inferred from molecular phylogenetic studies, pollination dominated by hopliine beetles evolved three times in the genus and long-proboscid fly pollination twice. We review the floral biology of the genus and provide full taxonomic accounts for all species, accompanied by illustrations, distributional information, conservation status and taxonomic history.

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