Adaptive radiation of pollination mechanisms in *Sparaxis* (Iridaceae: Ixioideae)

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ABSTRACT
Field observations, floral dissections, and nectar analyses of flowers, and pollen load analyses of floral foragers captured on 13 of the 15 *Sparaxis* species indicate that pollination systems are unusually diverse for such a small genus of Iridaceae endemic to southern Africa. The pollination ecology of *Sparaxis* can be divided into three overlapping systems, exploiting pollen vectors from three insect orders (Coleoptera, Diptera, and Hymenoptera). *Sparaxis auriculata*, *S. caryophyllacea*, *S. variegata* and *S. villosa* have zygomorphic, bilabiate, "gullet" flowers with stamens held against an erect or hooded dorsal tepal and are pollinated mainly by anthophorine bees (Apidae) and nectar is the primary reward. *Sparaxis metelerkampiae*, which has dark purple flowers with an elongate perianth tube, belongs to a local guild of species with similarly colored flowers pollinated by the long-proboscid fly *Prosoeca peringueyi* (Nemestrinidae). *Sparaxis parviflora*, with tiny, bilabiate, scented flowers, has exposed anthers and is pollinated by native honey bees foraging for pollen and nectar. The remaining species have actinomorphic perianths and narrow floral tubes that contain trace amounts of nectar. These are generalist species and they are visited by a broader range of insects, including hopliine scarab beetles, short-proboscid tabanid flies and, in some cases (*S. bulbifera* and *S. fragrans)* pollen-collecting bees. Outgroup comparison suggests that anthophorine bee pollination with nectar as the reward is ancestral in *Sparaxis.* Long-proboscid fly pollination has evolved at least once in the genus and a progression to increasingly symmetrical flowers in one clade has led from a generalist system using a variety of bee species in different families, hopliine beetles, and tabanid flies to a specialized system using only tabanid flies and hopliine beetles.

KEY WORDS
Iridaceae,
pollination,
floral presentation,
adaptive radiation.

RÉSUMÉ

Radiation adaptative des mécanismes de la pollinisation dans le genre Sparaxis (Iridaceae: Ixioideae).

Des observations de terrain, des dissections florales, des analyses du nectar, et l'examen du pollen prélevé sur des insectes visiteurs capturés dans les fleurs de 13 des 15 espèces de *Sparaxis*, montrent que les systèmes de pollinisation sont particulièrement diversifiés au sein de ce petit genre d'Iridaceae endémique d'Afrique australe. Trois systèmes de pollinisation, se chevauchant, impliquant des vecteurs polliniques appartenant à trois ordres d'insectes (Coléoptères, Diptères et Hyménoptères), peuvent être reconnus chez *Sparaxis.* Quatre espèces (*S. auriculata, S. caryophyllacea, S. variegata* et *S. villosa* possèdent des fleurs zygomorphes, bilabiées (de type « gosier ») dont les étamines sont appliquées contre un tépale dorsal érigé ou encapuchonné ; ces espèces sont pollinisées essentiellement par des abeilles (Anthophorinae : Apidae) pour lesquelles le nectar est le principal attrait. *Sparaxis metelerkampiae*, à fleurs pourpre-foncé à long tube périanthaire, appartient à un ensemble local d'espèces dont les membres possèdent des fleurs de couleur semblable pollinisées par une mouche à longue trompe, *Prosoeca peringueyi* (Nemestrinidae). *Sparaxis parviflora*, aux fleurs minuscules bilabiées et odorantes, à anthères apparentes, est pollinisé par des abeilles mellifères autochtones, attirées par le pollen et le nectar. Les autres espèces possèdent des fleurs à périanthe actinomorphe et à tube floral étroit qui contient des quantités infimes de nectar ; il s'agit d'espèces non spécialisées, visitées par un large éventail d'insectes dont des Scarabées (Hoppliinae), des Tabanidae à trompe courte et parfois des abeilles collectrices de pollen (chez *S. bulbifera* et *S. fragrans*). Une analyse phylogénétique suggère que la pollinisation par des Anthophorinae attirés par le nectar est le syndrome ancestral dans le genre *Sparaxis.* Au cours de l'évolution, il y a eu, au moins une fois, changement du système de pollinisation impliquant des mouches à longue trompe puis, dans un clade une évolution vers des fleurs de plus en plus actinomorphes, liée au développement d'un système spécialisé limité aux Tabanidae et aux Hopliinae à partir d'un système plus général impliquant des abeilles appartenant à diverses familles.

MOTS CLÉS
Iridaceae,
pollinisation,
présentation florale,
radiation adaptative.

INTRODUCTION

In most genera of Iridaceae native to southern Africa there is a positive correlation between species diversity and the diversity of pollination systems (BERNHARDT & GOLDBLATT 2000). Thus, the larger the genus the greater the number of pollination systems. For example, *Nivenia,* with only 10 species, is pollinated by long-proboscid flies in the genus *Prosoeca* (Nemestrinidae) and/or large-bodied, long-tongued anthophorine bees (GOLDBLATT & BERNHARDT 1990; GOLDBLATT 1997). In contrast, there are over 160 species in *Gladiolus* in southern Africa, with taxa pollinated by Apidae (bee taxonomy according to ROIG-ALSINA & MICHENER 1993) or passerine birds, or Lepidoptera, or long-proboscid flies, or andrenid and halictid bees, sometimes in combination with hairy scarab beetles (GOLDBLATT et al. 1998a; GOLDBLATT & MANNING 1998). Floral attractants, rewards, and functional morphology show great variation at both inter- and intrageneric levels because the pollinators of different species have such different foraging behaviors, capacities to detect colors and scents, and dissimilar mouthparts. At the inter- and intrageneric

level nectar analyses also indicate that different pollinators may have different sugar preferences. A genus containing less than 20 species rarely manifests more than two different pollination systems but genera with 25 or more species may have up to to six different pollination systems (GOLDBLATT & BERNHARDT 2000). For example, *Lapeirousia* (40 spp.) consists of species pollinated by long-proboscid flies, or anthophorine bees alone, or a combination of bees, diurnal Lepidoptera and scarab beetles, or nocturnal moths (GOLDBLATT et al. 1995). *Romulea* with 75 African species exploits scarab beetles alone, pollen collecting bees, a combination of beetles and bees, or in one case, long-proboscid flies (GOLDBLATT et al. 1998b; MANNING & GOLDBLATT 1996, and unpublished). The adaptive radiation of floral characters thus appears to have played a prominent role in speciation within lineages of African Iridaceae.

Sparaxis, a genus of Iridaceae subfamily Ixioideae described by KER GAWLER in 1802, and now including species in the past referred to *Streptanthera* and *Synnotia* (BAKER 1896), comprises just 15 species (GOLDBLATT 1992; GOLDBLATT & MANNING 1999). As presently circumscribed, *Sparaxis* is believed to be monophyletic and is defined largely by vegetative features, including leaf and floral bract morphology. Species extend from the Agulhas Peninsula in the south of the subcontinent to the Bokkeveld Plateau and western Karoo in the north, a range that falls entirely within the southern African winter-rainfall zone (BOND & GOLDBLATT 1984). Although *Sparaxis* comprises relatively few species compared, for example, with the estimated 255 species of *Gladiolus* or the 200 species of *Moraea* in sub-Saharan Africa, the ca. 50 species of *Ixia*, or the ca. 40 species of *Lapeirousia*, the genus exhibits a surprising range of floral forms (MANNING & GOLDBLATT 1997a), but very limited vegetative variation. Virtually all the variability in the genus lies in the flower and its associated reproductive system. Flowers range from short-tubed to long-tubed bilabiate forms to those with radially symmetric perianths with unilateral or symmetrically disposed stamens and styles. Perianth color ranges from violet with a yellow lower lip and throat, to entirely purple, mauve, white, yellow, or shades of red, orange or pink, then with a yellow center and usually conspicuous contrasting markings (Table 2). The androecium ranges from unilateral and arcuate in species with bilabiate flowers to unilateral or symmetric in species with symmetric perianths. The style diverges into three branches above the mouth of the floral tube and at or below the level of the anthers. Flowers vary from self-incompatible to facultatively self-compatible and several species routinely set full capsules of viable seeds in the absence of insect mediated pollen transfer (GOLDBLATT 1992).

Field studies of the pollination systems of *Sparaxis* species were undertaken as part of a continuing project to obtain pertinent information about trends in the floral evolution of the African Iridaceae. Analysis of pollination systems in this small genus permits comparisons with the role of adaptive radiation of pollination mechanisms in the larger genera.

MATERIAL AND METHODS

Floral phenology, life span, and floral presentation. — Direct observations of 14 of the 15 *Sparaxis* species were made during the years 1993 to 1999 in the field and in living collections at the Missouri Botanical Garden, St. Louis. Observations on the pollination biology of *Sparaxis* were made in the course of other field research in the southern spring at various sites (Table 1) in the southwestern Cape and the western Karoo, South Africa, areas of Mediterranean climate with wet winters and dry summers. Observation of insect foraging involved 4-12 hours per plant species and included recording of both floral attractants (pigmentation patterns, scent), mode and timing of anthesis (opening of individual buds), anther dehiscence, expansion of stigmatic lobes, behavior of insects on the flower, and taxonomic diversity of floral foragers.

Fragrance observations. — Floral scent was noted in the field and in cultivated plants. Scents too weak to be discerned by the human nose were recorded after individual flowers were picked and placed in clean, lidded glass jars and stored in a

Table 1. — Study sites and voucher information for species studied. Vouchers are housed at MO (GOLDBLATT) or at NBG (other collectors). All study sites in South Africa.

Species	Study site	Voucher
S. auriculata Goldblatt & J.C. Manning	Western Cape, Gifberg slopes	*Goldblatt & Manning 10966*
S. bulbifera (L.) Ker Gawl.	Western Cape, Darling	*Kurzweil 1272*
S. caryophyllacea Goldblatt	Western Cape, Nardouw Mts.	*Goldblatt 10671*
S. elegans (Sweet) Goldblatt	Northern Cape, Nieuwoudtville	*Lewis 5909*
S. fragrans (Jacq.) Ker Gawl.	Western Cape, Bot River	*Goldblatt & Manning 10012*
S. galeata Ker Gawl.	Western Cape, Vanrhyn's Pass	*Goldblatt 7234A*
S. grandiflora (Delaroche) Ker Gawl. subsp. *fimbriata* (Lam.) Goldblatt	Western Cape, Cape Town	*Goldblatt & Manning 9789*
subsp. *acutiloba* Goldblatt	Western Cape, N of Citrusdal	*Goldblatt & Manning 10368*
S. maculosa Goldblatt	not studied	
S. metelerkampiae (L. Bolus) Goldblatt & J.C. Manning	Western Cape, Pakhuis Pass	*Goldblatt & Manning 10386*
S. parviflora (G.J. Lewis) Goldblatt	Western Cape, Versveld Reserve, Darling	*Goldblatt & Manning 10358*
S. pillansii L. Bolus	Northern Cape, E of Nieuwoudtville	*Goldblatt & Manning 10429*
S. roxburghi (Baker) Goldblatt	Western Cape, N of Citrusdal	*Goldblatt & Manning 10333*
S. tricolor (Schneev.) Ker Gawl.	Northern Cape, Grasberg road, NW of Nieuwoudtville	*Goldblatt & Manning 10341*
S. villosa (Burm.f.) Goldblatt	Western Cape, near Malmesbury	*Goldblatt & Manning 10338*
	Western Cape, Darling Nature Reserve	*Goldblatt s.n.* (no voucher)
S. variegata (Sweet) Goldblatt	Western Cape, N of Clanwilliam	*Goldblatt 10568*

warm place. The contents of each jar were smelled after a minimum of 60 minutes (BUCHMANN 1983).

Nectar analysis. — Nectar volume measurements, reflecting both rates of secretion and depletion, were taken primarily from unbagged flowers in the field. To collect nectar whole flowers were picked and nectar was withdrawn from the bases of the perianth tubes with 3 µl capillary tubules after separating each ovary from the perianth base. The percentage of sucrose equivalents in fresh nectar was measured in the field or laboratory on a Bellingham & Stanley hand-held refractometer (0-50%) from five or more randomly selected flowering individuals per population, unless fewer individuals were available. Nectar samples were dried on Whatman filter paper no. 1 and sent to B.-E. VAN WYK, Rand Afrikaans University, Johannesburg, for HPTLC nectar chemistry analysis.

Analysis of compatibility systems. — Self-compatibility was determined by direct observations of greenhouse-grown plants at the Missouri Botanical Garden from which insects were excluded. This included an experimental series of self- and cross-pollinations made by hand. In addition, some tagged buds were permitted to open and wilt in the absence of hand manipulation to assess whether mechanical self pollination (autogamy) occurs.

Insect observation and pollen load analyses. — Insects visiting *Sparaxis* flowers were observed to determine included whether they contacted

anthers and stigmas while foraging. Insects observed probing the floral tube or brushing the anthers or stigmas were captured and killed in a jar using ethyl acetate fumes. Pollen was removed from insects after specimens were pinned. To prevent contamination of the body of an insect with pollen carried by another in the same jar, each insect was wrapped in tissue as soon as it was immobilized by jar fumes. Body length and proboscis length of insects were recorded from captured specimens. Capturing a fly at any site appeared to reduce the insect population significantly. We therefore killed as few individuals as necessary to obtain specimens for identification and pollen load analysis.

Removal of pollen from insect bodies was accomplished by gently scraping pollen off the body with a dissecting needle (see GOLDBLATT et al. 1995, 1998a). The residue from needle probes was collected on glass slides and mounted in 1-2 drops of CALBERLA's fluid (OGDEN et al. 1974). Pollen grains were identified microscopically by comparison with a reference set of pollen grain preparations made from plants flowering at study sites. *Sparaxis* pollen grains are recognized by their large size, perforate-scabrate exine, and monosulcate aperture with a prominent 2-banded operculum (GOLDBLATT et al. 1991) but they are indistinguishable from those of some other genera of Iridaceae, including *Gladiolus*. In the case of the flies, which are large insects, sites of pollen deposition are quite discrete for a particular plant visited and the pollen-providing species can usually be identified without recourse to microscopic examination.

Insect specimens were identified by R.W. BROOKS (Anthophoridae), C.D. MICHENER (Halictidae), University of Kansas, H. DOMBROW, Worms, Germany (Scarabaeidae), and J.C. MANNING (Diptera). Voucher specimens are deposited at the Snow Entomological Museum, Lawrence, Kansas.

RESULTS

Plant morphology and floral phenology. — Species of *Sparaxis* are seasonal, corm-bearing geophytes of small to moderate size, with spicate inflorescences typically 10-30 cm high, but up to 60 cm in *S. auriculata*. Individuals produce one or more simple or branched flowering stems annually and flowering is closely synchronized in a population. Flowering occurs in late winter and spring (July to October) (Table 2) which coincides with the period of optimal plant growth, during or soon after the main rainy season.

Flower buds open acropetally on an inflorescence. In all species a mature bud expands in the early to mid-morning and the open perianth typically lasts three or four days. Flowers open sequentially, usually one or two days apart; hence, there are often three or four flowers open at any time on an inflorescence. At sunset the flowers close, sometimes incompletely, but usually enclosing the anthers and stigmas. Flowers open again in the early morning, between 8.00 and 9.00 hours, depending on temperature.

Flowers of all species studied show weak mechanical protandry. The anthers dehisce longitudinally within one to four hours after the tepals first unfold but this depends to some extent on ambient temperature and humidity. Anthers may dehisce later the same day under wet, cool conditions. The three stylar lobes, the distal adaxial surfaces of which comprise the stigmas, are held together when the flower first opens and they diverge later during the same day. Once they have diverged, pollen will adhere to their slightly sticky surface.

Compatibility and self-pollination. — Studies of pollen-stigma compatibility of most species conducted under greenhouse conditions confirm the conclusions of HORN (1962) who showed that some species of *Sparaxis* are self-compatible (Table 2). Mechanical selfing is facilitated in most species by the absence of spatial separation of anthers and stigmatic surfaces after the style branches diverge. Specifically, the style divides opposite the lower half of the anthers and the lobes extend between the anthers, thus contacting the pollen directly. However, *S. auriculata*, *S. caryophyllacea*, *S. galeata* and *S. variegata* fail to set seed when self-pollinated by hand. In these species, coincidentally, the style divides at or shortly above the apex of the anthers, the style branches arch outward for up to 3 mm, and the

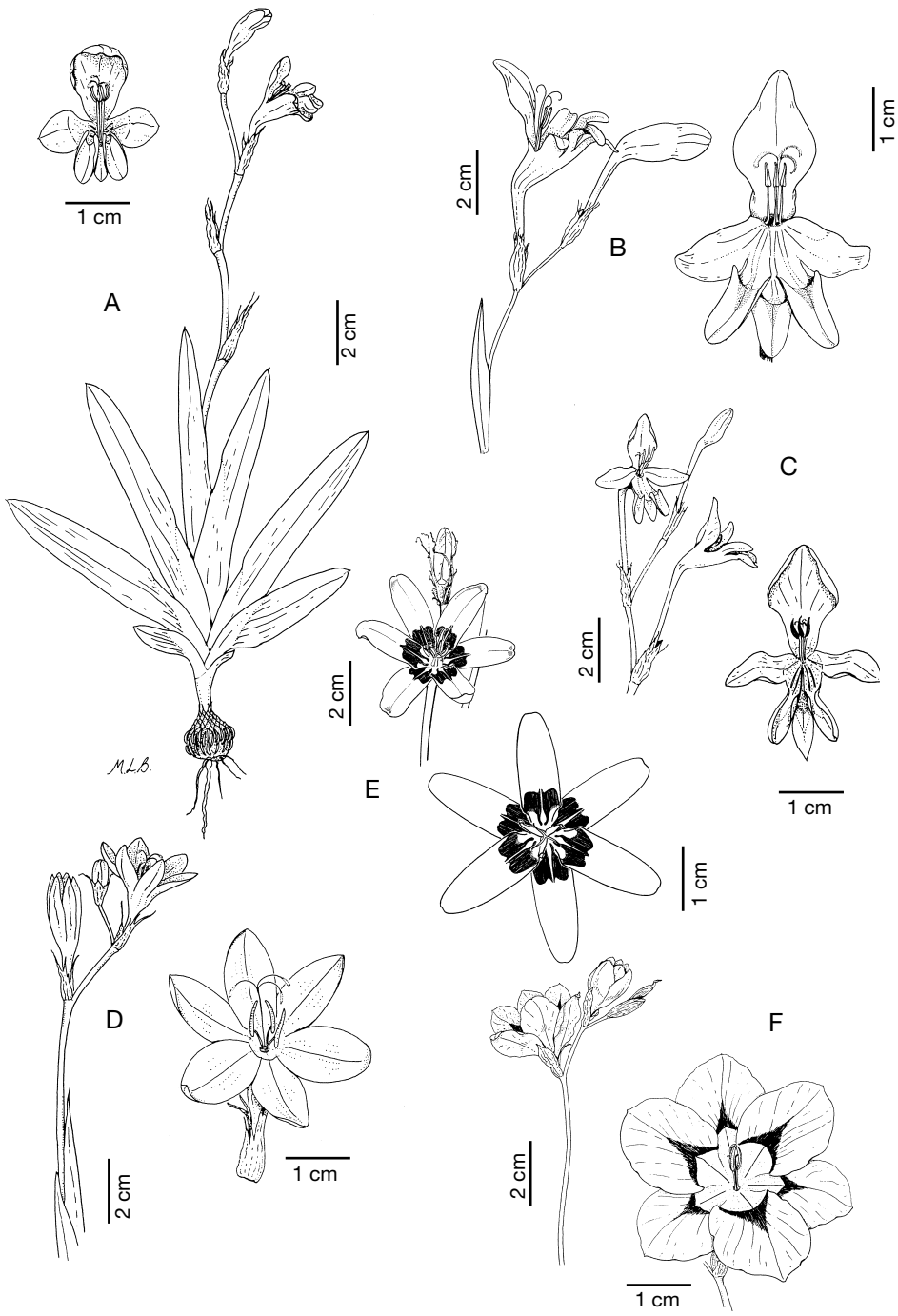

Fig. 1. — Flowers of ***Sparaxis*** species illustrating adaptations for different pollinators: **A,** *S. villosa* (anthophorine bees); **B,** *S. variegata* (anthophorine bees); **C,** *S. metelerkampiae* (long-proboscid flies); **D,** *S. bulbifera* (generalist: bees, hopliine beetles and short-proboscid flies); **E,** *S. maculosa* (hopliine beetles); **F,** *S. tricolor* (hopliine beetles and short-proboscid flies). Drawn by Margo L. Branch and John Manning.

style lobes do not contact the anthers or pollen (see illustrations in GOLDBLATT 1992).

Floral presentation and attractants. — Open flowers are typically held erect to suberect in a spike. Flowers are arranged helically in species with actinomorphic perianths or are secund in species with bilabiate perianths. *Sparaxis auriculata, S. caryophyllacea,* and usually *S. galeata* and *S. parviflora* have sweetly scented flowers, with an odor reminiscent of commercial *Viola odorata*. In some populations of *S. galeata* and *S. parviflora* the flowers appear to lack floral odor; those of *S. villosa* are consistently unscented. Flowers of *S. fragrans* have a musky, slightly bitter odor, unpleasant to the human nose. Flowers of all species have a well developed perianth tube (Table 2), ranging from ca. 8 mm in length in *S. elegans, S. pillansii,* and *S. tricolor* to 45-55 mm in *S. metelerkampiae*. Tubes are funnel-shaped with a narrow, tubular basal part 1-2 mm in diameter in species with radially symmetric flowers, or the tube may be cylindrical and elongate for up to 40 mm, then widening into a funnel-shaped upper part.

Floral colors and perianth shapes fall into four main categories (Table 2). In the first group, of which *Sparaxis auriculata* and *S. villosa* are typical examples, flowers are moderate in size, have a short, funnel-shaped floral tube and a zygomorphic, bilabiate perianth with a hooded dorsal tepal. The perianth is violet or mauve with the throat creamy yellow and the lower three tepals bright yellow, sometimes with contrasting violet tips. These flowers usually deposit nectar in the lower half of a hollow perianth tube. We were unable to detect nectar in flowers of *S. galeata*, and even when cut stems of this species were maintained in the laboratory in a flask of water the flowers did not produce nectar. *Sparaxis parviflora* is unusual in having particularly small flowers either colored purple and yellow, or more often cream with yellow lower tepals.

In the second group, the floral tube is elongate and the flowers are scentless, have an erect, flaglike dorsal tepal, and are either violet and yellow (*Sparaxis variegata*), cream with purple markings on the upper lateral tepals (*S. roxburghii*), or deep purple with pale streaks on the otherwise purple lower tepals (*S. metelerkampiae*).

Table 2. — Floral characteristics of *Sparaxis* species arranged according to flower type. Measurements of the perianth tube are for the lower cylindrical portion that excludes all but an insects proboscis. + = presence, - = absence, n/a = data not available, trace indicates nectar volume too little to measure volumetrically.

Species	Flower shape	Flower color	Lower tube (mm)	Tube open	Nectar	Self incompatible	Flowering time
S. auriculata	funnel	violet and yellow	ca.18	no	+	yes	Sep.
S. bulbifera	bowl	cream	12-16	yes	+	no	Sep.
S. caryophyllacea	funnel	violet and yellow	ca. 20	no	+	yes	Sep.
S. elegans	salver	salmon and purple	6-8	no	+	no	Aug.-Sep.
S. fragrans	salver	pale yellow or buff	6-8	no	trace	no	Aug.-Sep.
S. galeata	funnel	mauve and yellow	ca. 15	yes	–	yes	July-Aug.
S. grandiflora	salver	white, yellow or purple	10-14	no	trace	no	Aug.-Sep.
S. maculosa	salver	yellow, black center	ca. 2.5	no	n/a	n/a	Sep.
S. metelerkampiae	tube	dark purple	45-50	yes	+	no	Aug.-Sep.
S. parviflora	funnel	cream and yellow	ca. 8	no	trace	no	Aug.-Sep.
S. pillansii	bowl	rose pink and yellow	7-9	no	trace	no	Oct.
S. roxburghii	tube	mauve and yellow	20-30	yes	+	n/a	Sep.
S. tricolor	bowl	scarlet, yellow and black	ca. 8	no	trace	no	Sep.
S. variegata	tube	violet and yellow	30-35	yes	+	yes	Aug.-Sep.
S. villosa	funnel	violet and yellow	15-18	yes	+	no	Aug.-Sep.

The remaining two groups of species have radially symmetric, bowl- or salver-shaped, perianths but *Sparaxis bulbifera* and *S. grandiflora* have unilateral stamens. In *S. bulbifera* the perianth tube is 14-16 mm long, hollow, and contains nectar. The remaining six species of this group have a tube in which the walls tightly sheath the style, and only traces of nectar are present at the mouth of the tube. The flowers are uniform in color (cream to yellow, but purple in *S. grandiflora* subsp. *grandiflora*) or scarlet to salmon pink and then with contrasting markings in the center. *Sparaxis elegans* is unusual in having brown, twisted, sigmoid anthers. Flowers are odorless except in *S. fragrans* which produces a somewhat unpleasant, bitter, musk-like scent.

Nectar. — Nectar glands when present (Table 2) are septal, as they are in the entire subfamily Ixioideae (GOLDBLATT 1990, 1991 ; GOLDBLATT & MANNING, unpublished). Nectar is secreted from minute, circular pores at the top of the ovary, and flows directly into the base of the perianth tube where it is retained until removed by a foraging insect. In species with the lower part of the tube narrow and tightly enveloping the style (Table 2), a small amount of nectar, too small to measure, is often present in the upper part of the tube, presumably the result of capillary action. No nectar at all was detected in flowers of *S. galeata*. Measurable quantities of nectar are produced in seven of the 14 species examined for this character (Table 3). In the long-tubed *S. metelerkampiae* 1.4-3.6 µl of nectar were recorded. Nectar is sucrose rich to sucrose dominant with sugar solute making up 25-38% of the total volume of fluid.

Pollination mechanisms and pollen load analysis. — Pollination varies between *Sparaxis* species but correlates largely with the mode of floral presentation and nectar secretion. Short-tubed, zygomorphic flowers (group 1) are pollinated primarily by female *Anthophora diversipes*, which has a large body and a relatively long proboscis 6.5-8 mm long (GOLDBLATT et al. 1998a). These bees land on the flower and brush both the anthers and stigma lobes as they push their heads into the floral cup. The bees were not observed to scrape or manipulate anthers for pollen. *Anthophora diversipes* is a polylectic forager (Table 4) and individuals were found to carry the pollen of co-blooming Fabaceae, *Lachenalia* (Hyacinthaceae), *Salvia* sp. (Lamiaceae), *Lobostemon* (Boraginaceae), and Iridaceae (including *Gladiolus*, *Hesperantha*, *Homeria*) in their scopae. The foraging behavior of *A. diversipes* on *Sparaxis* species is indistinguishable from the pattern described for bee pollinated *Gladiolus* species (GOLDBLATT et al. 1998a), even in apparently nectarless *S. galeata*. The small flowers of *S. parviflora*, with exposed anthers, were visited exclusively by worker honey bees (*Apis mellifera*), which actively collected pollen. The presence of hopliine beetles on the flowers of *S. caryophyllacea* is unexpected and the beetles are most likely only occasional visitors. *Sparaxis caryophyl-*

Table 3. — Nectar properties of *Sparaxis* species that produce measurable quantities of nectar (Table 2); n/a = data not available. Nectar sugars were analyzed by B.-E. VAN WYK.

Species	Volume µl (n)	Mean% sugar (SD)	Fructose	Glucose	Sucrose	Mean Sucrose Glu+Fru (n)
S. auriculata	0.8-1.2(2)	39-42	n/a	n/a	n/a	n/a
S. bulbifera	1.2-1.8(3)	38.0(3.2)	13-15	17-18	68-70	2.19(3)
S. caryophyllacea	0.8-1.6(7)	26.1(2.8)	n/a	n/a	n/a	n/a
S. metelerkampiae	1.4-2.2(6)	28.5(3.4)	1-12	4-22	70-95	3.23(4)
sample 2	1.6-3.9(4)	25.8(1.9)	7-20	4-22	54-80	1.98(3)
S. roxburghii	1.3-1.8(3)	29.3(1.5)	n/a	n/a	n/a	n/a
S. variegata	1.2-2.4(10)	28.2(1.3)	n/a	n/a	n/a	n/a
S. villosa	1.1-1.5(7)	24.3(2.0)	n/a	n/a	n/a	n/a

Table 4. — Pollen load analysis of captured insects on sparaxies. Coleoptera: Scarabaeidae: *Anisochelus*, *Clania*, *Platychelus, Lepithrix, Peritrichia*. Hymenoptera: Apidae: *Anthophora*; *Apis*. Halictidae: *Petalapis*. Diptera: Nemestrinidae: *Prosoeca.* Tabanidae: *Mesomyia, Philoliche*.

Plant and [insect] taxon	**Number of insects carrying pollen load(s)**			
	Host flr. only	**Host flr. + other sp.**	**Other sp. only**	**No pollen**
S. auriculata				
[*Anthophora diversipes*]	0	2	0	0
S. bulbifera				
[*Apis mellifera*]	0	3	0	0
[*Lepithrix ornatella*]	0	2	0	0
[*Mesomyia edentula*]	2	2	0	0
S. caryophyllacea				
[*Anthophora diversipes*]	0	2	0	0
[*Anisochelus* sp.]	2	3	0	0
S. elegans				
[*Clania glenlyonensis*]	1	5	0	0
[*Anisochelus inornatus*]	0	5	1	0
[*Philoliche atricornis*]	0	6	0	0
S. fragrans				
[*Apis mellifera*]	0	3	0	0
[Halictidae]	0	2	0	0
[*Platychelus* sp.]	0	4	0	0
S. galeata				
[*Anthophora diversipes*]	0	1	0	0
S. grandiflora subsp. *acutiloba*				
[*Apis mellifera*]	0	2	0	0
[*Petallapis* sp.]	0	3	0	0
[*Philoliche atricornis*]	0	3	0	0
[*Peritrichia* sp.]	0	2	0	0
[*Anisochelus inornatus*]	2	4	0	0
[*Peritrichia rufotibialis*]	0	2	0	0
subsp. *fimbriata*				
[*Anisochelus inornatus*]	0	2	0	0
[*Peritrichia capicols*]	0	2	0	0
S. metelerkampiae				
[*Prosoeca peringueyi*]	0	3	0	0
S. parviflora				
[*Apis mellifera*]	2	3	0	0
S. tricolor				
[*Anisochelus inornatus*]	0	2	0	0
[*Philoliche atricornis*]	0	3	0	0
S. pillansii				
[*Clania glenlyonensis*]	1	7	1	1
[*Philoliche atricornis*]	0	2	0	0
S. variegata				
[*Anthophora diversipes*]	0	2	0	0
S. villosa				
[*Anthophora diversipes*]	0	5	0	0
Total	10	87	2	1

lacea shows none of the usual adaptations associated with hopliine beetle pollination.

Tubular flowers (group 2) were either visited by the long-proboscid fly, *Prosoeca peringueyi* (Nemestrinidae) on *Sparaxis metelerkampiae* or by *Anthophora diversipes* on *S. variegata*. The *Prosoeca* fly has a proboscis 32-35 mm long (MANNING & GOLDBLATT 1996) and it forages on the nectar held in the lower part of the perianth tube. These flies grasp the tepals with their tarsi and probe for nectar while continuing to vibrate their wings, contacting anthers and stigmas with the dorsal part of the thorax. Field observations and pollen load analyses show that *P. peringueyi* individuals visit *S. metelerkampiae* during the same foraging bouts in which they visit open flowers of *Pelargonium magenteum* (Geraniaceae), and species of Iridaceae including *Babiana geniculata* and *Lapeirousia jacquinii* (MANNING & GOLDBLATT 1996).

Sparaxis bulbifera is visited by a combination of worker honey bees, female halictid and andrenid bees, the tabanid fly, *Mesomyia*, and the hopliine scarab beetle, *Lepithrix ornatella*. The remaining species with bowl or salver-shaped flowers produce only traces of nectar and are visited by hopliine beetles and the short-proboscid tabanid fly *Philoliche atricornis* (proboscis 3–5 mm long) (Table 4). *Philoliche atricornis* was captured foraging for nectar on *S. grandiflora* subsp. *acutiloba*, *S. elegans* and *S. tricolor*, and carried either pure loads of *Sparaxis* pollen or mixed loads of pollen of *Sparaxis, Ornithogalum thyrsiflora* Jacq. (Hyacinthaceae), *Wurmbea* sp. (Colchicaceae), and Asteraceae. Beetles appeared to ignore the nectar in the floral tube, but sometimes foraged on pollen, contacting both dehisced anthers and stigma lobes during foraging, copulating, or engaging in agonistic behavior (see GOLDBLATT et al. 1998a). The foetid-smelling flowers of *S. fragrans* are pollinated by a combination of female halictid bees, worker honey bees, and the scarab beetle *Platychelus.*

For the two species for which we have not been able to obtain pollination data, we predict, on the basis of floral presentation, that flowers of *Sparaxis maculosa* are adapted for pollination by hopliine scarab beetles and those of *S. roxburghii* for pollination by long-proboscid flies.

DISCUSSION

The adaptive radiation of pollination mechanisms in *Sparaxis* obviously parallels that found in larger genera of the Iridaceae in southern Africa. Long-proboscid fly pollination involving *Prosoeca peringueyi* as found in *S. metelerkampiae* (and inferred for *S. roxburghii*), occurs in several other species of Iridaceae including *Babiana*, *Hesperantha*, *Lapeirousia,* and *Romulea* (GOLDBLATT et al. 1995; MANNING & GOLDBLATT 1996). Pollination by hairy hopliine beetles in *S. elegans, S. pillansii,* and *S. tricolor* exploits the same set of floral characters described by (GOLDBLATT et al. 1998b) in *Aristea*, *Ixia, Moraea*, and *Gladiolus meliusculus.* Bee pollination in the Iridaceae of southern Africa is a variable system (GOLDBLATT et al. 1998a; BERNHARDT & GOLDBLATT 1999) with floral characters and floral dimensions correlating with bee size, proboscis length, and foraging behavior. In this respect, pollination by *Anthophora diversipes* in *S. auriculata, S. caryophyllacea, S. variegata*, and *S. villosa* closely resembles the large-anthophorine bee system of pollination we have described in *Gladiolus* species with relatively short-tubed, gullet flowers.

In contrast, the pollination systems of *Sparaxis bulbifera, S. grandiflora*, and *S. fragrans* are less specialized and include a range of insects, including bees, scarab beetles, and tabanids. In *S. elegans, S. pillansii*, and *S. tricolor* both scarab beetles and tabanid flies appear to be the pollinators. This most resembles the bee-beetle pollination system in *Ixia tenuifolia* (GOLDBLATT et al. 1998b, as *I. framesii*) and *I. aurea* (GOLDBLATT & MANNING 1999).

Regardless of pollination system, most *Sparaxis* species are pollinated by insects that forage on a wide variety of co-blooming flowers. More than 90% of insects found to carry pollen of *Sparaxis* also carried the pollen of at least one other taxon of flowering plant. Polylectic and polyphagic foraging of insects that pollinate *Sparaxis* is comparable to similar modes of foraging described in the majority of irid genera distributed through southern Africa (BERNHARDT & GOLDBLATT 2000).

There is one apparently unique aspect of pollination in *Sparaxis*. Field and laboratory observa-

Fig. 2. — Selected ***Sparaxis*** species showing perianth shape and color differences associated with different pollinators: **A,** *S. villosa*; **B,** *S. metelerkampiae*; **C,** *S. bulbifera*; **D,** *S. grandiflora*; **E,** *S. tricolor*; **F,** *S. elegans* with the tabanid fly *Philoliche atricornis*.

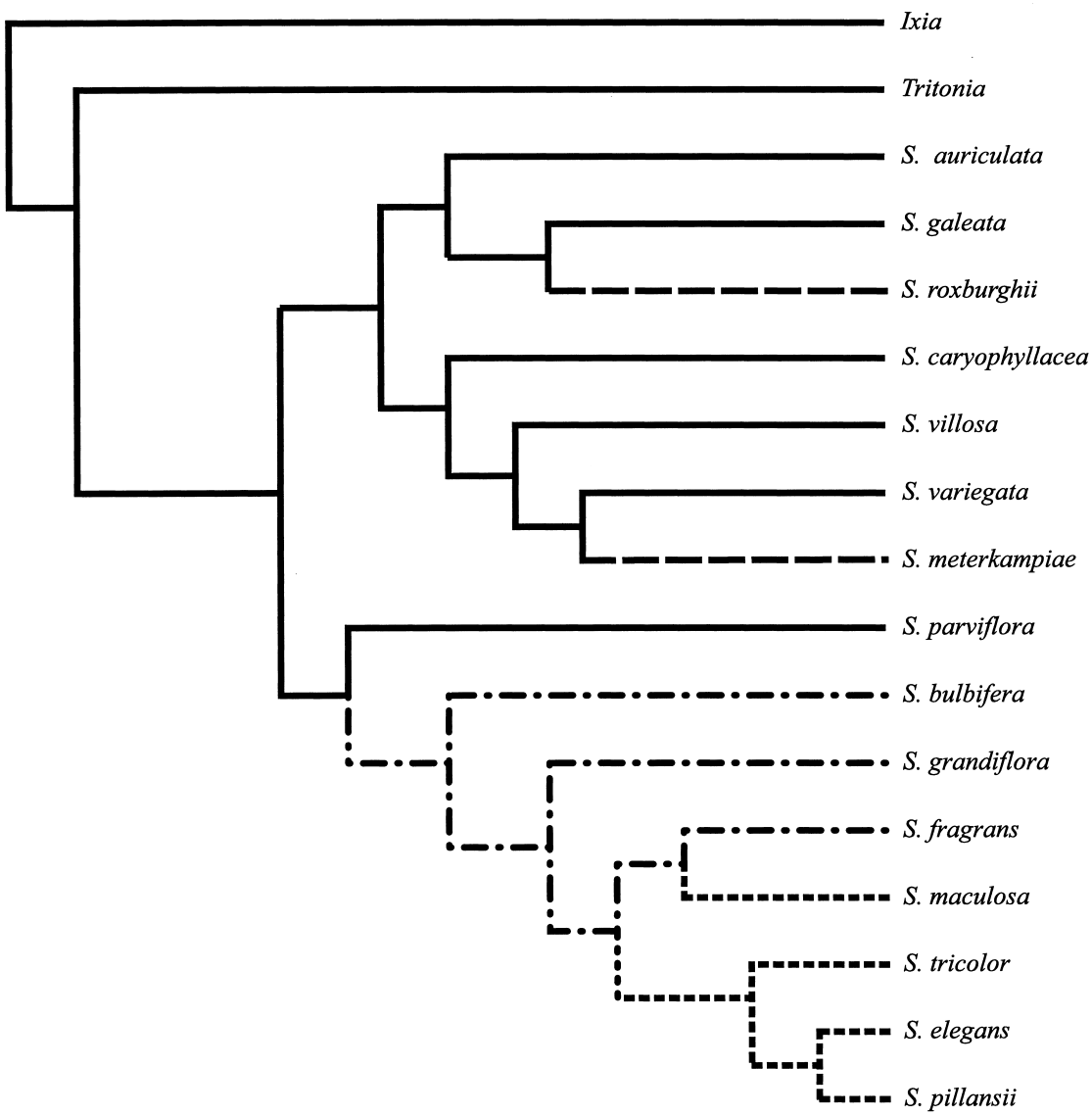

Fig. 3. — Evolution of pollination systems in ***Sparaxis*** mapped onto a phylogeny of the genus. The tree was obtained using the same characters as in GOLDBLATT (1992) but with a reversal of polarity for floral zygomorphy and orientation of flowers on the spike (now believed to be the character state for ancestors of *Sparaxis*) and the addition of the new species, *S. auriculata*. The tree is one of five produced using Henning 86 and the ie (implicit enumeration) and successive weighting options (consistency index, CI, 0.79). Solid line = the putative ancestral condition, bee pollination; long broken line = long-proboscid fly pollination (inferred for *S. roxburghii*); lines and dots = generalist pollination including hopliine beetles, honey and halictid bees, and tabanid flies; short broken line = strictly hopliine beetle and short-proboscid tabanid fly pollination (inferred for *S. maculosa*).

tions suggest that the flowers of *S. galeata* offer no reward to nectar seeking bees, but instead mimic flowers of a locally common species of *Gladiolus*, *G. venustus*, which does produce nectar (GOLDBLATT et al. 1998a). These flowers also broadly resemble those of other nectariferous species of *Sparaxis*. This mode of Batesian mimicry has been well discussed in the Orchidaceae (DAFNI & BERNHARDT 1989) but, to date, has not been documented in the Iridaceae. In *Orchis*, species with nectarless spurs are interpreted as mimics of nectariferous *Orchis* species (DAFNI & BERNHARDT 1989). This implies that guilds of insect-pollinated geophytes are so diverse and species rich in southern Africa that a *Sparaxis* species can successfully exploit the local bee fauna without offering a reward. Mimesis in *Sparaxis* then, converges with that of a number of *Disa* species (Orchidaceae), which also mimic floral presentation in floral guilds that include *Gladiolus*, *Pelargonium, Gladiolus,* and other species of Iridaceae (MANNING & GOLDBLATT 1997b; and see review in JOHNSON et al. 1998).

While pollination systems in *Sparaxis* are diverse, speciation in the genus is conservative compared to other southern African genera of the Iridaceae. The comparatively low number of species in *Sparaxis* cannot, we believe, be ascribed to massive past extinctions. The morphological evidence suggests that *Sparaxis* species are all closely allied, and do not reflect random survival of disparate taxa. Except for floral features, there is very little difference between most species of the genus.

If we map pollination systems on a reconstructed phylogeny of *Sparaxis* as done in *Lapeirousia* (GOLDBLATT & MANNING 1996) a similar pattern emerges (Figure 3). Outgroup comparison suggests that flowers of ancestral *Sparaxis* secreted nectar and were pollinated by anthophorine bees. Pollination by deceit and by long proboscid flies is more recently derived. A progression to increasingly symmetrical flowers in one clade is associated with a generalist system exploiting a combination of bees, hairy scarabs and short proboscid tabanid flies. In one of the terminal branches of this clade pollination appears to be accomplished by scarabs and tabanid flies alone. Thus in *Sparaxis* the evidence points to an anthophorine bee pollination system as ancestral and generalist or single-pollinator systems as derived. The pattern corresponds in general but not in detail to that in *Gladiolus* in which anthophorine bee pollination is also hypothesized to be ancestral.

In their treatment of pollination systems in the orchid genus *Disa*, JOHNSON et al. (1998) remark that most plant genera show a conservative range of pollination systems. That is, it is unusual to find more than one mode of animal pollination in a plant genus and when more than one mode is present, the transition between the two systems is generally minimal. For example, in *Pedicularis* (MACIOR 1982) the vast majority of species are pollinated by bumble bees (*Bombus*), and just a few species by small bodied solitary bees. This conservatism is obviously not reflected in *Sparaxis* even though it is a small genus of only 15 species compared to the more than 350 *Pedicularis* species. The conservatism of pollination systems within a plant genus, however, may simply reflect the opinion of systematists instead of the conservatism of real lineages. Systematists often treat floral characters like vegetative characters, subdividing lineages into separate genera based on similar floral traits that really reflect nothing more than shared pollination systems. For example, generic distinctions in the terrestrial orchids of the Mediterranean Basin are based primarily on floral characters despite the evidence of naturally occurring, partially fertile intergeneric hybrids (DAFNI & BERNHARDT 1989).

Modern phylogenetic treatments often show that while floral traits and pollination systems may appear unique they are often polyphyletic, nesting within larger lineages, e.g., *Disa* (JOHNSON et al. 1998), *Lapeirousia* (GOLDBLATT et al. 1995), *Gladiolus* (GOLDBLATT & MANNING 1998). Historically, *Sparaxis* sensu stricto was once divided into three different genera (BAKER 1896). One of these, the genus *Synnotia,* contained those *Sparaxis* species with bilabiate flowers pollinated by nectar-seeking anthophorine bees or long-proboscid flies. The monotypic *Streptanthera,* segregated a taxon that was pollinated by hopliine beetles and short-proboscid tabanids and merely had coiled anthers. Segregation of these genera obscures the evolutionary pattern of pollination diversification shown by the *Sparaxis* lineage.

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