Radiation of Pollination Systems in Gladiolus (Iridaceae: Crocoideae) in Southern Africa

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RADIATION OF POLLINATION SYSTEMS IN *GLADIOLUS* (IRIDACEAE: CROCOIDEAE) IN SOUTHERN AFRICA[1]

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ABSTRACT.

Pollination strategies adopted by the largely sub-Saharan African *Gladiolus* (approximately 260 species), one of the largest genera of the monocot family Iridaceae, are unusually diverse. The primary or sole pollinators include long-tongued apid and anthophorine bees (Apidae), short-tongued halictid and andrenid bees (Halictidae, Andrenidae), sometimes in combination with hopliine beetles (Scarabaeidae), long-proboscid flies (Nemestrinidae, Tabanidae), large butterflies (Satyridae), moths (mostly Noctuidae and Sphingidae), and sunbirds (Passerinae). Floral form correlates closely with pollination strategy, allowing us to infer the pollination ecology of almost all 165 species in southern Africa, although we have observations of animal visitors capable of accomplishing pollen transfer in only half this number. Pollination by apid bees foraging for nectar and passively transferring pollen brushed onto their bodies during feeding occurs in all seven sections of the genus in southern Africa and is also the most common strategy in five of these sections. Other pollinators include female bees actively foraging for pollen, or long-proboscid flies, sunbirds, moths, the satyrid butterfly, *Aeropetes*, all foraging for nectar, and in one species hopliine beetles that use the flowers as sites for assembly and copulation. Shifts in floral form associated with changes in pollination appear complex in the large flowers of *Gladiolus* species, but may in fact involve relatively simple developmental modifications, involving changes in perianth pigmentation, and often the type of marking on the tepals, presence or absence of scent, length of the perianth tube, and occasionally a shift from zygomorphy to actinomorphy. Associated with these changes is a correlated adjustment in nectar characteristics, including volume, sugar concentration, and sometimes sugar chemistry. With an inferred minimum of 32 shifts in pollination system in the 165 species in southern Africa, *Gladiolus* appears to have an unusually labile floral morphology, which may account for its extensive adaptive radiation.

Key words: bees, butterflies, floral ecology, *Gladiolus*, Iridaceae, long-proboscid flies, moths, nectar, pollination systems, sunbirds.

The pollination ecology of most genera of African Iridaceae is remarkably diverse (Bernhardt & Goldblatt, 2000). For example, in *Sparaxis* four different pollination systems have been described in 13 of its 15 species studied (Goldblatt et al., 2000a). In general, the larger the genus the greater the diversity of pollination systems. Thus, in *Lapeirousia* (Goldblatt et al., 1995), with almost half the species in the genus studied, five different pollination systems have been identified among 20 species. For the genus *Ixia*, with an estimated 50 species, six different systems have been described for 20 species (Goldblatt et al., 2000b). The genus *Gladiolus*, with some 255 species in Africa, is thus a primary target for the analysis of pollination systems as it is the largest genus in the family in Africa (Goldblatt, 1996; Goldblatt & Manning, 1998).

Seven distinct and, with few exceptions, non-overlapping pollination systems (Table 1) occur among the 80 *Gladiolus* species studied to date, which suggests that the range of pollination systems in *Gladiolus* may be wider than in any other genus of the Iridaceae in Africa and probably in the entire family. A general review comparing the pollination systems in *Gladiolus* is useful for two reasons. First, as usual, significant literature is scattered throughout technical journals, popular publications, and scientific monographs. Second, because widely different pollination systems occur in closely related species, a review of pollination in *Gladiolus* may make a useful model system for expanding our understanding of the adaptations associated with pollination shifts and how often pollination mechanisms change within a plant lineage.

Gladiolus is believed to be monophyletic, as circumscribed by Goldblatt and Manning (1998). It is defined largely on non-floral characters, the flowers being highly variable as they reflect direct adap-

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Table 1. Major floral types in *Gladiolus*. In pollen flowers tube length represents only the hollow (unblocked) upper part of the tube. Nectar sugar concentrations are ranges of means of samples of five to ten flowers in any species. Floral data are primarily from Goldblatt and Manning (1998); nectar data are from Goldblatt et al. (1998a, 1999) and Goldblatt and Manning (1999, 2002).

Flower type	Perianth shape	Perianth color	Perianth tube (mm)	Scent	Nectar volume (µl)	Nectar sugar conc. (%)	Dominant nectar sugar
Nectariferous bee	gullet or flag	Various, often bluish or pink, with dark streaks or yellow lip	12–20	Violet to rose or freesia	0.6–3.5(–6.0)	25–33(–40)	Sucrose
Pollen flower	rotate	Cream, yellowish or purple, without nectar guides	2.5–7	strong violet or none	ca. 0.5 or none	45.8	Sucrose
Long-proboscid fly	elongate gullet	Pink to cream with linear pink to red marks	(22–)30–100	none	2–12	25–30	Sucrose
Bird flower (*G. cunonius* clade)	gullet	Scarlet to crimson with green	12–20	none	6–27	18–27	Hexose
Bird flower (other clades)	flag (or gullet)	Scarlet to crimson	35–55	none	8–36	18–37	Sucrose
Moth flower	flag or gullet	White, cream or mottled brown	20–110	Sweet clove or fruity	4–12	(20–)30–36	Sucrose
Butterfly	flag (or gullet)	Scarlet to crimson, often with white splashes	35–55	none	4–20	18–27	Sucrose (rarely hexose)
Hopliine beetle	flag	Pink to orange with bold markings	ca. 10	Sweet violet	0.8–1.4	29.4	Sucrose

tations to particular pollination systems. The genus is defined by its unique ancestral basic chromosome number, $x = 15$, an inflated capsule, seeds with a broad circumferential wing, and a derived style in which the slender branches have expanded, bilobed tips that are conduplicate in bud and during the initial male phase of anthesis. The style appears to be the only floral feature that is apomorphic for the genus.

Distinctions between species, even those with different pollination systems, are relatively fine, although they appear highly visible in large-flowered plants such as *Gladiolus*. For example, the length and shape of the perianth tube, sometimes combined with a change in overall pigmentation, and details of the contrasting markings on the lower tepals (nectar guides) may signal a shift from apid-anthophorine bee to bird or long-proboscid fly pollination (Goldblatt & Manning, 1998; Goldblatt et al., 1998a, 1999). Tube length may be as short as 2.5 mm to as long as 120 mm. Floral pigmentation and patterning are extraordinarily diverse and flowers may be virtually any color and bear diverse types of nectar guides, including longitudinal or transverse banding, diffuse speckling, or no apparent contrasting marks. Nectars are mostly sucrose-dominant, but a few species of *Gladiolus* sect. *Hebea* have hexose-dominant nectar. Most species have a tube with nectar in the lower half, but a few have the tube tightly enveloping the style and do not secrete nectar. Flowers may be zygomorphic with unilateral, arcuate stamens and style, or the perianth may be actinomorphic with the stamens and style either symmetrically arranged or unilateral.

Several of these differences appear so gross that the affinities of highly specialized species were, in the past, often misunderstood, and *Gladiolus* species were segregated in several different genera based on a range of floral features now known to be adaptations for particular pollination systems. Thus, *Acidanthera* included some *Gladiolus* species with white to pink, long-tubed flowers, and *Anomalesia, Homoglossum, Kentrosiphon,* and *Oenostachys* included species with bright red, long-tubed flowers, with the bracts, tepals, and floral tube modified in different ways. It is now known that *Acidanthera* was a polyphyletic assemblage of plants with flowers adapted for pollination by moths or long-proboscid flies. Its constituent species have been transferred to several genera, including *Babiana, Geissorhiza,* and *Hesperantha* (Goldblatt, 1984, 1985), although the type species is now included in *Gladiolus* (Goldblatt, 1996). In contrast, *Anomalesia, Homoglossum, Kentrosiphon,* and *Oenostachys* comprise species with flowers adapted for pollination by sunbirds (Goldblatt, 1996; Goldblatt & Manning, 1998), all now believed to be nested within different sections of *Gladiolus*. The reduction of these genera and the resulting reclassification of their species results in an entirely different picture of the adaptive radiation of a monophyletic group. What emerges is that in certain genera, of which *Gladiolus* is the prime example, the "correct" classification, that is, a monophyletic one, is vital to the interpretation of the adaptive radiation of a clade. In *Gladiolus* relatively minor structural modifications to suites of floral features cause pollination systems to change dramatically. In contrast to genera like *Pedicularis* (Scrophulariaceae), where changes in floral features alter the mode of pollination but not the pollinators (Macior, 1982, 1984), floral changes in *Gladiolus* often alter the pollen vectors radically, shifting pollination from one order of insects or birds to another.

Field studies of selected species of *Gladiolus* from different sections of the genus and including examples of several species of each of the main flower types show that flower type from whatever section closely correlates with pollination strategies (Johnson & Bond, 1994; Goldblatt et al., 1998a, b, 1999; Goldblatt & Manning, 1998, 1999, 2002). This allows us to infer pollination strategies of all but a few of the 165 species of *Gladiolus* that occur in southern Africa, site of most of the pollination studies so far conducted in the genus. Comparing pollination strategies in the genus with the phylogenetic classification proposed by Goldblatt and Manning (1998) makes it possible to infer, to a large extent, the patterns of floral radiation and associated pollination shifts that have occurred in the genus. This in turn permits us to gauge with some measure of confidence the evolutionary lability in pollination strategies and the extent to which ancestral floral morphology determines pollination system.

FLORAL DIVERSITY IN *GLADIOLUS*

Although species of *Gladiolus* exhibit a wide range of floral form and are particularly variable in perianth pigmentation, all share one important feature relating to their pollination ecology, a perianth tube. In most species, the tube forms a reservoir for nectar secreted from septal nectaries. Additionally, all but two of the southern African species (*G. quadrangulus* and *G. stellatus*) have unilateral stamens and styles, with the anthers normally exserted from the tube and arched below the dorsal tepal. Based on extensive field study and research for systematic monographs of the genus in tropical and southern Africa (Goldblatt, 1996; Goldblatt & Manning, 1998), we recognize seven major floral types, each with a different set of floral traits closely correlating with a particular pollination system. The most significant floral features include the shape and dimensions of the floral tube, perianth pigmentation, and the shape and color of the markings (nectar guides) on the lower tepals. Similar floral types do not always indicate shared relationship but are consistently associated with a particular pollination system (e.g., Goldblatt et al., 1995, 1999; Goldblatt & Manning, 1999; Manning & Goldblatt 1996, 1997). Vegetative morphology appears to be a more reliable guide to species relationships. The major floral types (Table 1) are as follows:

Group 1. Nectariferous bee flowers (Fig. 1A, B) include species with a zygomorphic, bilabiate perianth with an obliquely funnel-shaped tube mostly 12–20 mm long, usually slightly shorter than the arching to hooded dorsal tepal (gullet flowers sensu Faegri & van der Pijl, 1979) or sometimes the dorsal tepal is erect and prominent (flag flowers sensu Faegri & van der Pijl). The perianth tube consists of a flared upper portion that tapers to a narrow cylindrical lower half. Small amounts of nectar, secreted from septal nectaries, are retained in the lower, cylindrical half of the tube, which is usually 6–12 mm long. Nectar is sucrose-rich, ranges in volume from 0.6 to 3.5(to 6) μl per flower, and has a concentration mostly of 25–33%, but up to 40%, sucrose equivalents (88 species) (Goldblatt et al., 1998a).

Species of the southern African summer- and winter-rainfall zone show several differences among the flowers of this group. In the summer-rainfall zone, flowers are usually relatively small, ca. 20–25 mm long, rarely scented, and are numerous and crowded on straight spikes. The tepals are mostly colored shades of pink, orange, or mauve, and usually bear nectar guides of low contrast with the base perianth color (species of sects. *Densiflorus*, *Heterocolon*, *Linearifolius*, and *Ophiolyza*).

In the winter-rainfall zone flowers are medium-sized to relatively small and 25–35 mm long, are almost always scented, and are usually few to several, mostly on flexuose spikes. The tepals are often colored shades of blue to mauve or pink, but also scarlet, yellow, green, or brown, and the lower tepals usually bear prominent nectar guides of a variety of shapes, depending on taxonomic affiliation. Nectar guides may consist of uniform pale color on the proximal half of the tepals (sect. *Hebea*) or of pale color with irregularly streaked dark longitudinal lines and dots, or transverse bands of pale and dark color (sect. *Homoglossum*, sect. *Linearifolius*).

Group 2. Pollen flowers (Fig. 1C, D) are characteristically small, ca. 20 mm long, with an actinomorphic, mostly rotate perianth, and a tube less than 8 mm long or if longer completely closed internally due to the walls of the tube being closely wrapped around the style. The tepals are often dull-colored (cream, yellowish, or light purple), lack obvious nectar guides, and the stamens and style are unilateral or symmetrically placed in the center of the perianth. The flowers are scented or not, and secrete small to minute amounts of nectar or are nectarless. Species are restricted to winter-rainfall southern Africa in sections *Hebea*, *Homoglossum*, and *Linearifolius* and flower in the spring (4 species) (Goldblatt et al., 1998a).

Group 3. Long-proboscid fly flowers (Fig. 1E, F) have a medium to large perianth, mostly 45–80 mm long and an elongate, cylindrical perianth tube (22–)30–100 mm long, slightly to much exceeding the dorsal tepal. Few to several flowers are borne on straight spikes and have cream to pink tepals with reddish nectar guides of linear or spear-shaped marks in the middle of the tepals. The anthers and pollen are often unusually colored, and dark purple. Flowers always lack scent, but produce large amounts of sucrose-rich to sucrose-dominant nectar, mostly of 2–12 μl in volume and 25–30% sucrose equivalents per flower. Species occur throughout southern Africa, mostly of section *Blandus*, but there are also examples from sections *Densiflorus*, *Hebea*, *Homoglossum*, and *Ophiolyza* (29 species). Those of the winter-rainfall zone flower in late spring to summer, after peak flowering of the flora; in the summer-rainfall zone species flower in the late summer and autumn, coinciding with the end of the flowering peak in the flora (Goldblatt & Manning, 1999, 2000).

Group 4. Bird flowers (Fig. 1G, H) are represented by species with a large perianth, mostly 50–80 mm long, with an elongate tube, usually 35–55 mm long, as long as or longer than the dorsal tepal, the tube often narrow below, broad and cylindrical above (Table 1). The gullet or flag flowers lack nectar guides, are unscented, and the tepals are scarlet to crimson, sometimes partly yellow or green on the lower tepals. Plants often have well-exserted anthers borne on sturdy filaments, a stout stem, and an erect, straight spike bearing enlarged floral bracts. Flowers secrete large amounts of nectar, mostly sucrose-dominant (sects. *Ophiolyza* and *Homoglossum* series *Homoglossum*) and with 29–35% sucrose equivalents per flower, or sucrose rich (*G. priorii*: sect. *Homoglossum*) and 18–25% su-

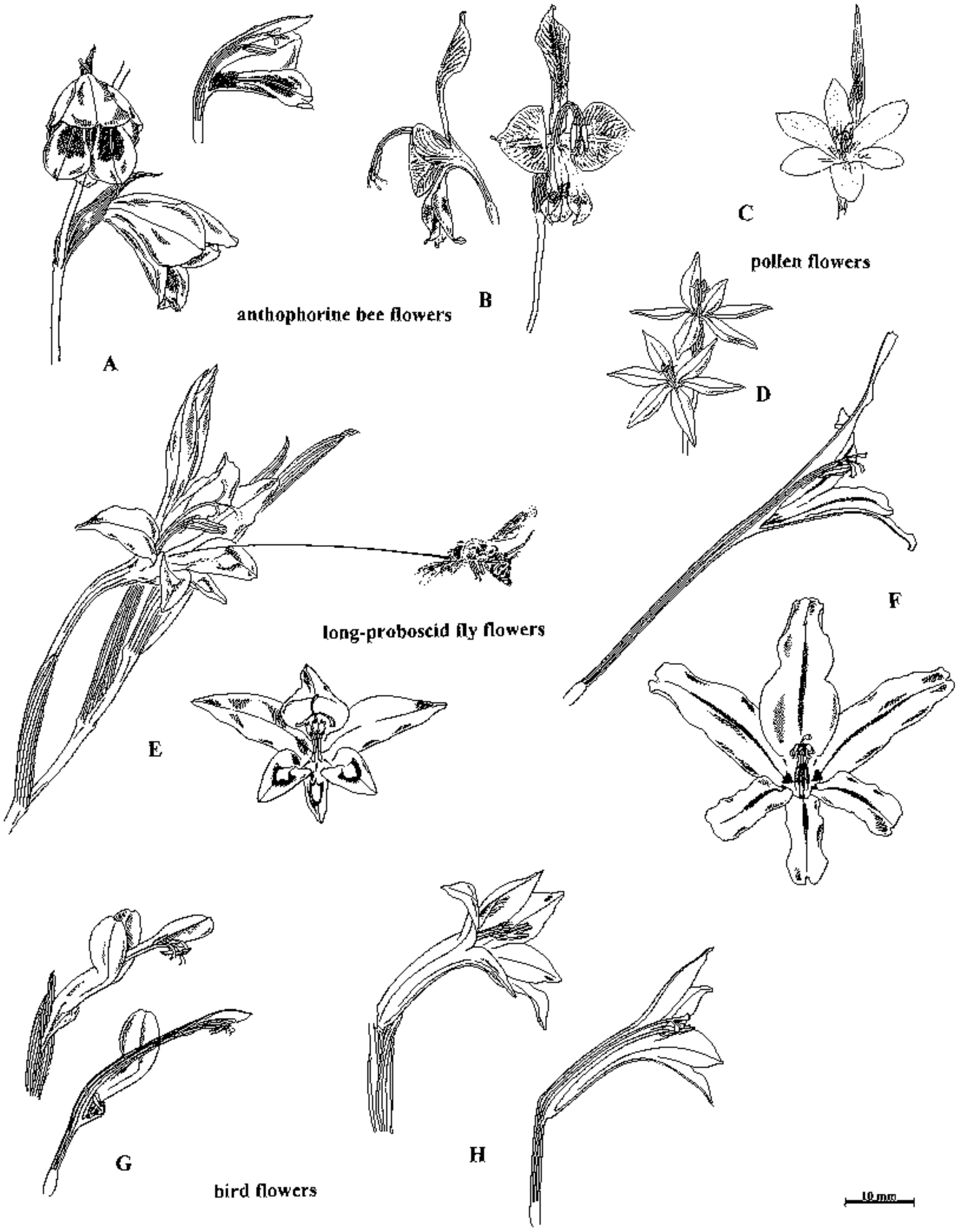

Figure 1. Examples of anthophorine bee flowers (A, B), pollen flowers (C, D), long-proboscid fly flowers (E, F), and bird flowers (G, H) in *Gladiolus*. —A. *G. papilio* (sect. *Densiflorus*). —B. *G. uysiae* (sect. *Hebea*). —C. *G. quadrangulus* (sect. *Homoglossum*). —D. *G. stellatus* (sect. *Hebea*). —E. *G. angustus* (sect. *Blandus*) and its pollinator, *Moegistorhynchus longirostris*. —F. *G. floribundus* (sect. *Blandus*). —G. *G. cunonius* (sect. *Hebea*). —H. *G. watsonius* (sect. *Homoglossum*). Scale bar 10 mm. Drawn by John Manning.

crose equivalents. Nectar volumes may be as much as 36 μl in *G. watsonius* (sect. *Homoglossum*) (Goldblatt & Manning, 1998; Goldblatt et al., 1999).

Flowers differ extensively among clades in this group. In section *Hebea*, bird pollinated species allied to *G. cunonius* (Table 1) have a perianth tube 12–20 mm long, the lower tepals reduced to scale-like dimensions, the dorsal tepal is much enlarged, the anthers are tailed, and the style branches stigmatic only at the rounded tips. They also produce relatively dilute nectar of 18–27% sucrose equivalents that contains a predominance of glucose and fructose, a sharp contrast to bird flowers of other sections. Bird pollinated *Gladiolus* species occur throughout southern Africa, mainly section *Homoglossum* in winter-rainfall southern Africa and flowering in the winter or spring, or section *Ophiolyza* in eastern southern Africa and flowering in the late spring and summer (20 species).

Group 5. Moth flowers (Fig. 2C—F) are found in species with a medium-sized to fairly large perianth and a cylindrical or gradually flared perianth tube, 20–110 mm long, somewhat to much exceeding the dorsal tepal (Table 1). The perianth is colored white to cream or alternatively, heavily speckled dull brown, with nectar guides obscure or evidently lacking (UV reflectance was not tested). Flowers are richly scented, sometimes only in the evening, and produce 4–12 μl of sucrose-dominant nectar, mostly 30–36%, but only 20–22% in *Gladiolus emiliae* and 24–28% in *G. longicollis*. An odd feature of several of these species are relatively short stamens, the anthers often partly included in the floral tube. Species are from four sections, notably series *Tristis* of section *Homoglossum*, and mostly restricted to winter-rainfall southern Africa, flowering from early spring to early summer, thus coinciding with the peak flowering of the flora (9 species) (Goldblatt & Manning, 1998, 2002).

Group 6. Satyrid butterfly flowers (Fig. 2A, B) are found in species with a large perianth, mostly exceeding 50 mm long, with a more or less cylindrical perianth tube and unilateral stamens, the latter included in the tube in *Gladiolus nerineoides*. The tube is slightly longer than the tepals, 35–55 mm long, but slender (as opposed to wide in the upper half in bird flowers). The tepals are reddish (scarlet to crimson), usually with white guides on the lower tepals (contrasting with absence of marking in bird flowers). The flowers are unscented, and produce ample amounts of sucrose-rich to sucrose-dominant nectar of moderate concentration, 18–27% sucrose equivalents and 4–20 μl in volume per flower (Table 1). Some species, including *G. cruentus* and *G. saundersii*, stand out among insect pollinated *Gladiolus* in having hexose-rich nectar. Flowering in the summer from mid-December to April, species occur mostly in winter-rainfall southern Africa, mostly of section *Blandus* but also section *Linearifolius*, with a few in summer-rainfall southern Africa (and tropical Africa), belonging to section *Ophiolyza* (9 species) (Johnson & Bond, 1994; Goldblatt & Manning, 1998, 2002).

Group 7. Hopliine beetle flowers occur in species with a moderate-sized perianth with a short perianth tube, ca. 10 mm long (Table 1). The tepals are brightly colored (either deep pink or orange) mostly with bold markings in yellow and purple (painted bowl flowers of Bernhardt, 2000) and show less pronounced zygomorphy, compared to immediate relatives, thus tepals are less unequal in size. Flowers secrete small amounts of nectar, bloom in the spring, and are restricted to winter-rainfall southern Africa (1 species) (Goldblatt et al., 1998b; Goldblatt & Manning, 1998).

PHENOLOGY

Flowering phenology is an important consideration in understanding the patterns of diversification of pollination systems in southern African *Gladiolus*. The subcontinent has two dramatically contrasting climate regimes, a warm wet summer and dry, cold winter in central and eastern southern Africa and a cool wet winter and hot, dry summer in the southwest. Species of *Gladiolus* occur in both zones but nearly all are restricted to only one. In the summer-rainfall zone species flower in the late spring, summer, and autumn, whereas in the winter-rainfall zone species may flower at any season. Even in the summer-dry winter-rainfall zone there are locally mesic habitats that support *Gladiolus* species flowering in the summer. Other summer- or autumn-flowering species bloom before foliage leaves are produced, an adaptation in the winter-rainfall zone that has significant consequences for pollination there.

POLLINATOR CLASSES AND THEIR DISTRIBUTION

Field observations of floral visitors have shown a consistent pattern throughout southern Africa in the correlation between flower type and pollinator class, although individual species in each pollination class may differ, especially in the summer- versus the winter-rainfall parts of the subcontinent. The following pollinator classes have been recognized based on field observation, capture (excepting birds), and identification of visiting insects (Johnson & Bond, 1994; Goldblatt et al., 1998a; Gold-

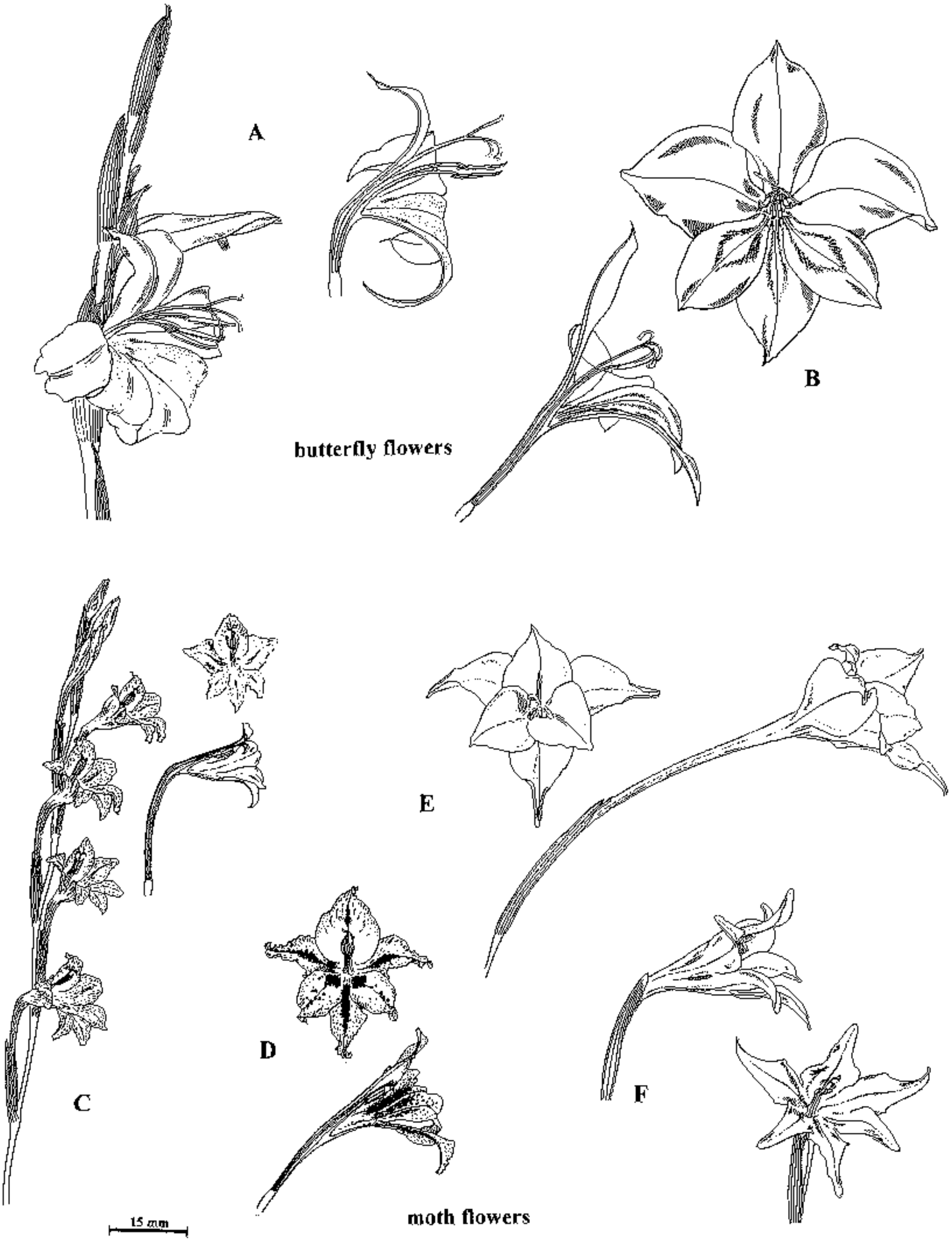

Figure 2. Examples of butterfly flowers (A, B) and moth flowers (C–F) in *Gladiolus*. —A. *G. saundersii* (sect. *Ophiolyza*). —B. *G. sempervirens* (sect. *Blandus*). —C. *G. emiliae* (sect. *Linearifolius*). —D. *G. maculatus* (sect. *Homoglossum*). —E. *G. longicollis* (sect. *Homoglossum*). —F. *G. tristis* (section *Homoglossum*). Scale bar 15 mm. Drawn by John Manning.

blatt & Manning, 1998, 1999; Manning & Goldblatt, 1995, and in prep.). Visitors were identified as pollinators (Table 2) when they had the appropriate size and shape to access floral nectar, brushed against the sexual organs of the flower during visits, and had been confirmed (by microscopic and sometimes direct visual examination) to be carrying pollen of the species visited on the appropriate part of their bodies so that stigmatic surfaces of flowers would brush against carried pollen on subsequent visits.

1. Long-tongued bees. Various large-bodied, long-tongued bees of the family Apidae s.l. (including Anthophoridae) (Roig Alsina & Michener, 1993), mainly *Amegilla*, *Anthophora*, sometimes *Apis*, and occasionally *Pachymelus*, *Tetralonia*, and *Xylocopa*, are the primary or exclusive visitors to 42 species (and are inferred for another 46 species) belonging to group 1, i.e., gullet or flag flowers of small to moderate size with tubes fairly short and obliquely funnel-shaped (Table 2). This is true irrespective of taxonomic grouping and phytogeography (Goldblatt et al., 1998a). These bees have bodies 10–17 mm long and 4–7 mm wide across the thorax, and mouthparts 4–10 mm long. Flowers show a close fit between size and shape and a bee's body. The flared upper tube is mostly 8–10 mm long and snugly accommodates a bee's head and thorax, while the narrow, cylindrical part, mostly 6–10 mm long, admits only the slender mouthparts. To reach the nectar, bees climb into the flower and push their mouth parts into the narrow part of the tube. As they maximally extend their tongues so that they can reach the nectar, their upper body is pressed against the anthers, which lie under the dorsal tepal. Pollen is then brushed onto the dorsal part of the thorax and sometimes the head or dorsal part of the abdomen. When stigmas are unfolded (then assumed to be receptive), usually on the last day a flower is open and when pollen has usually been removed (Goldblatt et al., 1998a), the stigmatic surfaces lie in the same position as the anthers, and are then ideally positioned for pollen to be deposited passively on their sticky surfaces as a bee visits the flower to feed on nectar.

Neither the base color of the flower nor the form of the contrastingly colored nectar guides appear significant in this pollination system, but the presence of nectar guides is so consistent that we assume it serves an important function, perhaps of orienting the bee so that it approaches the flower in a consistent manner so that pollen is effectively deposited dorsally on the body. The reward in these bee pollinated flowers is nectar, always present in moderate quantities and always sucrose-rich to sucrose dominant (Goldblatt et al., 1998a).

Often, the same bee species has been collected on flowers of a wide range of color and scent characteristics, suggesting that variation in size, pigmentation, scent, and form of the nectar guide outlined for group 1 has little direct significance in relation to pollinator. For example, the most common bee that we have recorded visiting *Gladiolus* flowers in western southern Africa in spring, *Anthophora diversipes*, visits species of almost any color and nectar guide configuration. Thus visual signals of ground color, nectar guide, and odor are not significant to pollinators. Likewise, the most common bees in eastern southern Africa, *Amegilla fallax* and *A. capensis*, both visit and can evidently pollinate many of the species there with flowers of this type.

In addition to bees, the flowers of group 1 are occasionally visited by the short-proboscid flies, *Psilodera* (Acroceridae) and *Prosoeca* (Nemestrinidae), with probosces 10–14 mm long. Their body and mouthpart size is similar to that of a large bee, and these nectar feeders function as pollinators just as effectively as long-tongued bees (Goldblatt et al., 1997, 1998a). Other visitors to these flowers include hopliine beetles (Scarabaeidae: Hopliini), which appear to be unimportant for most *Gladiolus* species, and we regard them as vandals rather than even secondary pollinators.

Except for a few isolated examples, notably *Gladiolus trichonemifolius* in which pollen appears to be an important reward, species are used mainly as sources of nectar and are visited by both male and female bees. Female bees use many other plants as pollen sources for nest provisioning (including co-blooming Asphodelaceae, Boraginaceae, Hyacinthaceae, Fabaceae, Malvaceae, Oxalidaceae, and Polygalaceae). The brighter and more varied coloration and frequent production of scent in the winter-rainfall zone versus the dull, less variable coloration and absence of scent in summer-rainfall eastern southern Africa (and tropical Africa), irrespective of taxonomic affiliation, is notable. This pattern holds even in section *Linearifolius*, the only section widely shared between the two areas. We have hypothesized that when flowers are dull-colored and appear (to the human eye) to blend with the surrounding vegetation and soil surface (Goldblatt et al., 1998a) scent may be the primary attractant. Otherwise, bright coloration combined with a distinctive odor may help flowers compete for pollinators in the winter-rainfall zone where flowering in the flora is concentrated in a few weeks in spring. In the summer-rainfall zone the flower season is more protracted, and fewer species bloom at any particular time.

The significance of floral odor is often underestimated. Bees learn to discriminate among different odors six times more rapidly than they do colors (Schoonhoven et al., 1998) and can readily distinguish between numerous, similar odors. Thus the presence and variety of scents among co-blooming species alone may encourage floral constancy even when flowers are visually similar.

This type of bee pollination is the most common pollination strategy in *Gladiolus* (Table 3). It occurs in all seven taxonomic sections, and it is the most common one in sections *Densiflorus*, *Hebea*, *Heterocolon*, *Homoglossum*, and *Linearifolius*. Some 53% of the southern African species have flowers adapted for this system (Tables 3, 4). Elsewhere, we have postulated that anthophorine bee pollination is ancestral in *Gladiolus* (Goldblatt et al., 1998a; Goldblatt & Manning, 1999).

2. *Short-tongued bees or worker honey bees.* The short-tongued bee, *Andrena* sp., visits the fragrant flowers of *Gladiolus stellatus*, while *Apis mellifera* is the only bee species captured on actinomorphic *G. quadrangulus* and zygomorphic *G. aureus*. Both bees actively collect pollen, prominently displayed in erect anthers. In *G. stellatus* the flowers are particularly strongly scented. Flowers of *G. brevitubus* are zygomorphic, with unilateral stamens, but have a floral tube less than 3 mm long and evidently lack nectar. Only small halictid bees, ca. 6 mm long, have been captured on these flowers, which appear to offer pollen as the sole reward to insect visitors. Although short-tongued andrenid bees have been captured while visiting *Gladiolus meliusculus*, hopliine beetle species are more consistent and frequent visitors and so, we assume, are more important in the pollination of this species (Goldblatt et al., 1998b). This is discussed in detail below.

Pollination by small- or large-bodied female bees foraging for pollen as the primary pollination strategy is evidently found in only four southern African species of the genus (Goldblatt et al., 1998a). The system occurs in section *Hebea* (*Gladiolus stellatus*), section *Homoglossum* (*G. quadrangulus*: series *Carinatus*, and *G. brevitubus*: series *Brevitubus*), and section *Linearifolius* (*G. aureus*), evidently having evolved convergently four times (Table 4).

3. *Long-proboscid flies.* Long-proboscid flies with mouthparts mostly 20–60 mm long in two families, Nemestrinidae (tangle-veined flies) and Tabanidae (horseflies), have proven to be important pollinators (Table 2) of many southern African plant species with long floral tubes (Goldblatt et al., 1995; Manning & Goldblatt, 1996, 1997; Goldblatt & Manning, 1999). Long-proboscid flies have been found to be the sole visitors to *Gladiolus* species belonging to group 3, i.e., odorless, cream to pink flowers with an elongate tube and producing ample, sucrose-rich to -dominant nectar (Table 1). Typically only one species of fly at a particular site, occasionally two, visits a species. In the eastern southern African highlands, the late summer-flying *Prosoeca ganglbaueri* is the sole pollinator of at least *G. oppositiflorus*, *G. microcarpus*, *G. mortonius*, and *G. varius*. A fifth species, *G. calcaratus*, with a somewhat shorter tube, is also visited by this fly, but its tongue is so long that its body does not brush the anthers when it forages for nectar. The long-proboscid fly *Prosoeca robusta*, also on the wing in late summer, appears to be the main pollinator of *G. calcaratus*. Another fly, *Stenobasipteron wiedmannii* (also Nemestrinidae), is the sole visitor and presumably pollinator of the long-tubed *G. macneilii* in lower-altitude habitats in eastern southern Africa where *P. ganglbaueri* and *P. robusta* seem absent.

Along the south coast of South Africa the nemestrinid fly *Prosoeca longipennis* appears to be the sole pollinator of the long-tubed *Gladiolus bilineatus* and *G. engysiphon* that flower in the autumn. In western southern Africa, species with flowers of group 3 are visited by the tabanid *Philoliche rostrata* (*G. floribundus*, *G. monticola*, *G. undulatus*, *G. vigilans*), the nemestrinids *Moegistorhynchus longirostris* (*G. angustus*) and *M.* sp. (*G. rhodanthus*), either *Prosoeca nitidula* and *Philoliche rostrata* or both (*G. carneus*, *G. monticola*). Remarkable among long-proboscid flies, *M. longirostris* has a proboscis up to 80 mm long and the *Gladiolus* species that it pollinates, *G. angustus*, has a cream perianth with red markings and a tube 80–100 mm long.

Long-tongued flies are present in southern Africa mostly in the warmer months, October to April, and hence plant species pollinated by these insects are constrained to this flowering period. Furthermore, different species of fly are active at different times of the year. These flies are nectar feeders, and they acquire pollen loads from the flowers they visit passively. The remarkable similarity in flower color and the shape of the nectar guides in unrelated species of *Gladiolus* pollinated by long-proboscid flies suggests that there is an important adaptive value to floral conformity in long-tongued fly pollination systems.

Sixteen species of *Gladiolus* have to date been confirmed as being pollinated by long-proboscid flies (Table 3). An additional 13 species with similar floral morphology are inferred to have the same pollination strategy, thus 29 species, 18% of south-

Table 2. *Gladiolus* species and their confirmed pollinators and other floral visitors. Abbreviations: Coleop = Coleoptera, Dipt = Diptera, Hym = Hymenoptera, Lepid = Lepidoptera, Nemestr = Nemestrinidae, Passer = Passerinae, Scarab = Scarabaeidae. Data are from Goldblatt et al. (1998a, 1999) and Goldblatt & Manning (1999, 2000) except for the pollinator of *G. debilis*, *Prosoeca westermannii*, which is a novel report herein.

Species	Primary pollinator	Taxonomic affinity (order and family)	Secondary pollinator(s)	Thieves & vandals
Section *Densiflorus*				
G. appendiculatus G. J. Lewis	*Amegilla aspergina*	Hym: Apidae	—	*Prosoeca robusta*
G. calcaratus G. J. Lewis	*Prosoeca robusta*	Dipt: Nemestr	*Amegilla capensis*	*Prosoeca ganglbaurii*
G. crassifolius Baker	*Amegilla capensis,* *A. spilostoma*	Hym: Apidae Hym: Apidae	*Prosoeca* sp.	—
G. densiflorus Baker	*Amegilla fallax*	Hym: Apidae	—	*Prosoeca robusta*
G. exiguus G. J. Lewis	*Amegilla fallax,* *A. spilostoma*	Hym: Apidae Hym: Apidae	—	*Prosoeca robusta*
G. ferrugineus Goldblatt & J. C. Manning	*Amegilla aspergina,* *A. capensis*	Hym: Apidae Hym: Apidae	—	—
G. macneilii Oberm.	*Stenobasipteron wiedmannii*	Dipt: Nemestr	—	—
G. microcarpus G. J. Lewis	*Prosoeca ganglbaurii*	Dipt. Nemestr	—	—
G. mortonius Herbert	*Prosoeca ganglbaurii*	Dipt: Nemestr	—	—
G. papilio Baker	*Amegilla aspergina,* *A. capensis,* *Tetralonia* sp.	Hym: Apidae Hym: Apidae Hym: Apidae	—	—
G. varius F. Bolus	*Prosoeca ganglbaurii*	Dipt: Nemestr	*P. robusta*	—
Section *Ophiolyza*				
G. dalenii van Geel	*Nectarinia afra,* *N. famosa*	Aves: Passer Aves: Passer	—	—
G. dolomiticus Oberm.	*Amegilla spilostoma,* *Xylocopa rufitarsus*	Hym: Apidae Hym: Apidae	*Lasioglossum* sp.	*Allodape variegata*
G. ecklonii Lehm.	*Amegilla aspergina,* *A. capensis*	Hym: Apidae Hym: Apidae	—	—
G. flanaganii Baker	*Nectarinia famosa*	Aves: Passer	—	—
G. oppositiflorus Herbert	*Prosoeca ganglbaurii*	Dipt: Nemestr	—	—
G. saundersii Hook. f.	*Aeropetes tulbaghia*	Lepid: Satyridae	—	—
G. sericeovillosus Hook. f.	*Amegilla spilostoma*	Dipt: Nemestr	*Prosoeca* sp.	—
Section *Blandus*				
G. angustus L.	*Moegisorhynchus longirostris*	Dipt: Nemestr	—	—
G. bilineatus G. J. Lewis	*Prosoeca longipennis*	Dipt: Nemestr	—	—
G. cardinalis Curt.	*Aeropetes tulbaghia*	Lepid: Satyridae	—	—

Table 2. Continued.

Species	Primary pollinator	Taxonomic affinity (order and family)	Secondary pollinator(s)	Thieves & vandals
G. carneus D. Delaroche	*Philoliche rostrata,* *Prosoeca nitidula*	Dipt: Tabanid Dipt: Nemestr	—	*Amegilla spilostoma*
G. floribundus Jacq.	*Philoliche rostrata* and/or *P. gulosa*	Dipt: Tabanid Dipt: Tabanid	—	—
G. grandiflorus Andrews	*Anthophora diversipes*	Hym: Apidae	—	—
G. phoenix Goldblatt & J. C. Manning	*Amegilla spilostoma*	Hym: Apidae	—	—
G. sempervirens G. J. Lewis	*Aeropetes tulbaghia*	Lepid: Satyridae	—	—
G. stefaniae Oberm.	*Aeropetes tulbaghia*	Lepid: Satyridae	—	—
G. undulatus L.	*Philoliche rostrata*	Dipt: Tabanid	—	—
Section *Heterocolon*				
G. marlothii G. J. Lewis	*Anthophora diversipes*	Hym: Apidae	—	—
G. mostertiae L. Bolus	*Amegilla obscuriceps*	Hym: Apidae	—	—
G. rufomarginatus G. J. Lewis	*Amegilla langii,* *A. spilostoma,* *Stenobasipteron difficile*	Hym: Apidae Hym: Apidae Dipt: Nemestr	—	—
Section *Linearifolius*				
G. aureus Baker	*Apis mellifera*	Hym: Apidae	—	—
G. brevifolius	*Amegilla obscuriceps,* *A. spilostoma,* *Psilodera valida*	Hym: Apidae Hym: Apidae Dipt: Acrocerid	*Allodape exoloma* *A. pictifrons*	*Lipotriche* sp.
G. emiliae L. Bolus	*Hippotion celerio,* *Cucullia extricata*	Lepid: Sphingid Lepid: Noctuid	—	—
G. guthriei F. Bolus	*Cucullia inaequalis*	Lepid: Noctuid	—	*Macaria simplicilinea,* *Hypagoptera* sp.
G. hirsutus Jacq.	*Apis mellifera*	Hym: Apidae	—	*Anisonyx ursus*
G. monticola G. J. Lewis ex Goldblatt & J. C Manning	*Philoliche rostrata,* *Prosoeca nitidula*	Dipt: Tabanid Dipt: Nemestr	—	*Amegilla spilostoma*
G. nerineoides G. J. Lewis	*Aeropetes tulbaghia*	Lepid: Satyridae	—	—
G. rhodanthus J. C. Manning & Goldblatt	*Moegistrohynchus* sp.	Dipt: Nemestr	—	—
Section *Hebea*				
G. alatus L.	*Anthophora diversipes*	Hym: Apidae	*Rediviva aurata*	—
G. arcuatus Klatt	*Apis mellifera*	Hym: Apidae	—	—

Table 2. Continued.

Species	Primary pollinator	Taxonomic affinity (order and family)	Secondary pollinator(s)	Thieves & vandals
G. ceresianus L. Bolus	*Anthophora diversipes*	Hym: Apidae	—	—
G. cunonius (L.) Gaertn.	*Nectarinia chalybea*	Aves: Passer	—	—
G. equitans Thunb.	*Pachymelus peringueyi*	Hym: Apidae	—	—
G. meliusculus (G. J. Lewis) Goldblatt & J. C. Manning	*Lepisia rupicola,*	Coleo: Scarab	*Andrena* sp.	—
	Pachycnema crassipes	Coleo: Scarab		
G. orchidiflorus Andrews	*Anthophora diversipes*	Hym: Apidae	—	—
G. permeabilis D. Delaroche	*Anthophora diversipes*	Hym: Apidae	—	—
G. saccatus (Klatt) Goldblatt & M. P. de Vos	*Nectarinia famosa,*	Aves: Passer	—	—
	N. fusca	Aves: Passer		
G. scullyi Baker	*Anthophora diversipes*	Hym: Apidae	—	—
G. speciosus Thunb.	*Rediviva aurata*	Hym: Melittidae	—	—
G. stellatus G. J. Lewis	*Andrena* sp.	Hym: Andrenidae	—	—
G. uysiae L. Bolus ex G. J. Lewis	*Anthophora diversipes*	Hym: Apidae	—	—
G. venustus G. J. Lewis	*Anthophora diversipes,*	Hym: Apidae	—	—
	A. krugeri	Hym: Apidae		
G. virescens Thunb.	*Anthophora diversipes*	Hym: Apidae	—	—
G. watermeyeri L. Bolus	*Anthophora diversipes*	Hym: Apidae	—	—
	A. krugeri	Hym: Apidae		
Section *Homoglossum*				
G. abbreviatus Andrews	*Nectarinia famosa*	Aves: Passer	—	—
G. blommesteinii L. Bolus	*Anthophora diversipes*	Hym: Apidae	—	—
G. brevitubus G. J. Lewis	*Lasioglossum* sp.	Hym: Halictidae	—	—
G. carinatus Aiton	*Anthophora diversipes*	Hym: Apidae	*Lasioglossum* sp.	—
	A. krugeri,	Hym: Apidae		
	A. schulzei	Hym: Apidae		
	Apis mellifera	Hym: Apidae		
G. debilis Sims	*Prosoeca westermannii*	Dipt: Nemestr	—	—
G. engysiphon G. J. Lewis	*Prosoeca longipennis*	Dipt: Nemestr	—	—
G exilis G. J. Lewis	*Amegilla fallax*	Hym: Apidae	—	—
G. gracilis Jacq.	*Anthophora diversipes,*	Hym: Apidae	*Xylocopa rufitarsus*	*Anisonyx ursus*
	Apis mellifera	Hym: Apidae		
G. griseus Goldblatt & J. C. Manning	*Apis mellifera*	Hym: Apidae	—	—
G. inflatus Thunb.	*Amegilla obscuriceps*	Hym: Apidae	—	—
G. inflexus Goldblatt & J. C. Manning	*Anthophora krugeri,*	Hym: Apidae	—	—

Table 2. Continued.

Species	Primary pollinator	Taxonomic affinity (order and family)	Secondary pollinator(s)	Thieves & vandals
	Apis mellifera, *Patellapis* sp.	Hym: Apidae Hym: Halictidae		
G. jonquilliodorus Eckl. ex G. J. Lewis	*Amegilla spilostoma*, *Apis mellifera*	Hym: Apidae Hym: Apidae	—	—
G. liliaceus Houtt.	*Cucullia extricata*	Lepid: Noctuidae	—	*Tyromoptes inferior*
G. longicollis Baker	*Agrius convolvuli*	Lepid: Sphingidae	—	—
G. maculatus Sweet	*Cucullia terensis*	Lepid: Noctuidae	—	—
G. martleyi L. Bolus	*Amegilla spilostoma*	Hym: Apidae	—	—
G. meridionalis G. J. Lewis	*Nectarinia violacea*	Passer: Nectarinid	—	—
G. quadrangulus (D. Delaroche) Barnard	*Apis mellifera*	Hym: Apidae	—	—
G. patersoniae F. Bolus	*Anthophora diversipes*, *A. krugeri*	Hym: Apidae Hym: Apidae	*Apis mellifera*	—
G. recurvus L.	*Hippotion eson*	Lepid: Sphingidae	*Anthophora diversipes*	—
G. sufflavus (G. J. Lewis) Goldblatt & J. C. Manning	*Anthophora diversipes*	Hym: Apidae	—	—
G. trichonemifolius Ker-Gawl.	*Apis mellifera*	Hym: Apidae	—	—
G. tristis L.	*Cucullia* sp.	Lepid: Noctuidae	—	—
G. vigilans Barnard	*Philoliche rostrata*	Dipt: Tabanidae	—	—
G. virgatus Goldblatt & J. C. Manning	*Philoliche rostrata*	Dipt: Tabanidae	—	—

Table 3. Analysis of the frequency and taxonomic distribution of the pollination systems in southern African species of *Gladiolus*. Southern African species comprise 165 species distributed in 7 sections and 27 series, all believed to be monophyletic based on morphological analysis (Goldblatt & Manning, 1998); n/a = not applicable.

Pollination System	Total species confirmed	Total confirmed and inferred	Taxonomic sections	Taxonomic series
Large-bodied, long-tongued bees (Apidae s.l.)	39	87 (53%)	7	22
Short-tongued (or pollen-collecting) bees	4	4 (2%)	3	3
Long-proboscid fly	16	29 (18%)	6	13
Passerine bird	6	20 (12%)	4	7
Moth	6	11 (7%)	3	5
Satyrid butterfly	5	9(5%)	3	3
Hopliine beetle (short-tongued bee)	1	1 (<1%)	1	1
Uncertain	4	4 (2%)	n/a	n/a

ern African *Gladiolus*, are inferred to be adapted for pollination by long-proboscid flies. Long-proboscid fly pollination thus appears to be the second most common pollination strategy in the genus, after nectariferous bee pollination (Goldblatt & Manning, 1999, 2000). The strategy occurs in six of the seven sections of the genus and it is the most common one in section *Blandus*, elsewhere occurring in isolated species. In section *Densiflorus* long-proboscid fly pollination occurs in one or two species of three series, in sections *Homoglossum* and *Hebea* in three species each belonging to a different series, and in one species of sections *Linearifolius* and *Ophiolyza*. For the present, long-proboscid fly pollination is assumed to have arisen only once in any series, though this is by no means established. This suggests parallel evolution of long-proboscid fly pollination a minimum of 12 times.

4. Sunbirds. *Gladiolus* flowers adapted for pollination by sunbirds have been identified in five sections of the genus (Goldblatt et al., 1999). The flowers conform to the classic type in Africa that are pollinated by sunbirds, *Nectarinia* (Table 2), a genus of passerine birds that feed on nectar as well as insects (Rebelo et al., 1987). Although the flowers in species of each section are broadly similar in their red color and production of large amounts of nectar, they differ in significant details, including perianth tube shape, size of the lower tepals relative to the dorsal, presence or absence of contrasting markings, and nectar sugar chemistry (Goldblatt & Manning, 1998).

In section *Homoglossum* all six species of series *Homoglossum* and two of series *Mutabilis* appear to have flowers adapted for sunbird pollination. These species all have a long tube, the upper part of which is wide and cylindrical (presumably to accommodate a bird's bill), and the species produce fairly concentrated nectar that is sucrose-dominant, a stark contrast to the bird flowers in section *Hebea* and many other bird pollinated flowers. Most of the remaining species of *Gladiolus* in southern Africa

Table 4. Taxonomic distribution of pollination systems in southern African *Gladiolus*. Lp fly = Long-proboscid fly.

Gladiolus section (total species)	Pollination system—known/plus predicted							
	Bees							
	Passive	Active	Lp fly	Bird	Moth	*Aeropetes*	Hopliine beetle	Uncertain
Section *Densiflorus* (20)	6/12	0	5/8	0	0	0	0	0
Section *Ophiolyza* (15)	2/6	0	1/1	2/5	0	1/2	0	1
Section *Blandus* (21)	2/6	0	5/8	0/1	0	3/5	0	1
Section *Linearifolius* (17)	2/7	1/1	2/2	0/2	2/2	1/2	0	1
Section *Heterocolon* (9)	3/8	0	0	0	0	0	0	1
Section *Hebea* (32)	12/21	1/1	0/3	2/4	0/2	0	1/1	0
Section *Homoglossum* (51)	12/27	2/2	3/7	2/8	4/7	0	0	0
Total 165	39/87	4/4	16/29	6/20	6/11	5/9	1/1	4
% total	53%	2%	18%	12%	7%	5%	<1%	2%

adapted for bird pollination belong in section *Ophiolyza*, the most well known of which is the widespread *G. dalenii* (also in Madagascar and tropical Africa). This species has been reported by Vogel (1954) to be visited by *Nectarinia afra* (greater double-collared sunbird), and we recorded *N. famosa* foraging actively on *G. dalenii*. The high Drakensberg *G. flanaganii* has also been recorded as visited by *N. famosa*. Observations of visits by birds to the six species of series *Homoglossum* are limited to sightings of *N. famosa* visiting *G. abbreviatus*. In section *Hebea*, visits to *G. saccatus* (a western southern African species) by *Nectarinia famosa* and *N. fusca* and to *G. cunonius* (a southern coastal species) by *N. chalybea* have been noted (Goldblatt & Manning, 1998). We did not try to capture avian visitors of any bird pollinated species but confined ourselves to observation of visitors and analysis of floral nectar.

Bird pollinated flowers occur in five species of section *Ophiolyza*, four species in one series of section *Hebea*, eight species in two series of section *Homoglossum*, two species in one series of section *Linearifolius*, and one species of section *Blandus*, a total of 20 species, 12% of the southern African species. In series *Mutabilis* of section *Homoglossum* it is not yet established whether the bird pollinated species *G. meridionalis* and *G. priorii* are a clade or are independently derived from a common ancestor (Goldblatt & Manning, 1998). In bird pollinated species, markedly different inflorescence or floral adaptations confirm the independent origin of the strategy. In section *Hebea* three species of bird pollinated flowers have the style branches apically stigmatic and anthers with long sterile tails, in addition to hexose-rich to hexose-dominant nectar, unique adaptations in the genus. In section *Homoglossum* series *Homoglossum* the spike is straight and relatively thick, whereas in series *Mutabilis* the spike is fairly slender and flexuose (an ancestral feature found in other members of this section). For want of firm evidence to the contrary, we assume that bird pollinated members of section *Ophiolyza* are a monophyletic group and represent a single origin of the strategy. We hypothesize that bird pollination arose at least six times in *Gladiolus* and possibly seven.

5. *Night-flying moths.* A variety of moths have been captured visiting species with flowers of group 5, and included species of two families, Noctuidae and Sphingidae (Table 2). The syndrome is difficult to document because the moths are active at night and hence difficult to catch or even to see. Sphinx moth pollination occurs in *G. longicollis* in eastern southern Africa (*Agrius convolvuli*), both sphinx and noctuid moths (species of the genera *Hippotion* and *Cucullia*) pollinate several species of the winter-rainfall west of the subcontinent, and species of the noctuid *Cucullia* have been captured on *G. guthriei*, *G. liliaceus*, and *G. maculatus*. An unidentified species of Sphingidae also visited *G. liliaceus* but avoided capture. We saw few other insects visiting any putatively moth pollinated species during many hours of observation, day and night, but a male anthophorid bee, *Anthophora diversipes*, was captured while visiting *G. recurvus* (I. Nänni, pers. comm.), a species apparently adapted for moth pollination. The bee attempted to forage on nectar of this species, flowers of which are scented during the day as well as the night. The bee is evidently not the normal visitor but appears capable of accomplishing pollination although unable to reach the nectar in the long perianth tube.

Moths are poor pollen vectors, as their bodies are covered with loose scales to which pollen appears to adhere loosely. However, all the moths captured carried visible amounts of *Gladiolus* pollen on the upper parts of their probosces (Goldblatt & Manning, 2002). When the flowers are in the female phase, on the last of four or five days of anthesis, the stigmatic lobes lie in the same position as the anthers, and pollen adhering to a moth's proboscis is then optimally placed for passive transfer to the exposed stigma lobes. There seems no obvious distinction between species pollinated by sphingids versus noctuids except perianth tube length. In the longer-tubed *G. longicollis*, tube length, 65–110 mm long in subspecies *platypetalus*, prevents successful nectar foraging by most noctuids.

Some 11 southern African species in three different sections of *Gladiolus* (7% of the southern African total—Tables 3, 4) have flowers of group 5, and observations on six of them (Goldblatt & Manning, 1998, and in prep.) confirm that they can correctly be categorized as being adapted for moth pollination. Moth pollinated flowers are inferred for two species of section *Hebea* (*G. robertsoniae* and *G. acuminatus*, which according to morphological comparison (Goldblatt & Manning, 1998) are distantly related members of series *Permeabilis*); section *Homoglossum* (*G. maculatus*, *G. albens*, and morphologically very different and presumably distantly related *G. recurvus*: series *Gracilis*, and four of the five species of series *Tristis*); and section *Linearifolius* (*G. emiliae* and *G. guthriei*: series *Linearifolius*). We suggest that the strategy most likely arose six times, once in section *Linearifolius*, twice in section *Hebea* and three times in section *Homoglossum*.

6. Large butterflies. A single species of butterfly, *Aeropetes tulbaghia* (Satyridae), appears to pollinate species of group 6, those with red flowers, usually with white markings on the lower tepals. This butterfly has an innate affinity for bright red colors and is the sole or major pollinator of a guild of red-flowered species that bloom in the late summer in southern Africa (Johnson & Bond, 1994). We have recorded *Aeropetes* visiting *G. cardinalis*, *G. nerineoides*, *G. saundersii*, *G. sempervirens*, and *G. stefaniae*. Both *G. cardinalis* and *G. sempervirens* have already been reported in the literature to be pollinated by *Aeropetes* (Johnson & Bond, 1994). Demonstration of this pollination syndrome is difficult because population sizes of *Aeropetes* vary considerably from year to year, and individuals may be absent locally in some seasons. Hence, populations of some species of *Gladiolus* may not be visited and pollinated at all in some years. We assume this to be the case in 1995 when we attempted to identify the pollinator of *G. cruentus* and *G. insolens*, which we infer from floral morphology to be adapted for pollination by *Aeropetes* (or in the case of *G. cruentus*, perhaps some other large butterfly).

Butterfly flowers in *Gladiolus* superficially resemble those adapted for bird pollination. Butterflies and birds do not, however, normally share any *Gladiolus* species, and in the winter-rainfall part of southern Africa they cannot, for no bird pollinated *Gladiolus* species there flowers when *Aeropetes* is on the wing in late summer. Apart from phenology, flowers pollinated by *Aeropetes* have a narrower tube than do flowers pollinated by birds and so do not permit entry of a bird's bill. The white splashes on most *Gladiolus* species pollinated by *Aeropetes* are not a feature of any bird pollinated members of the Iridaceae excepting *G. flanaganii*, and this is the only species of the genus in which both *Aeropetes* and sunbirds are recorded as visitors (Johnson & Bond, 1994). The firm texture of the floral parts, rigid stem, and hooded dorsal tepal suggest sunbird pollination is its primary strategy. At least in the winter-rainfall zone butterfly flowers appear to have evolved from fly pollinated ancestors where the phylogenetic relationships can be inferred, as in series *Blandus* (Goldblatt & Manning, 1998).

As in long-tongued bee, long-proboscid fly, and moth pollination systems, the reward offered to butterflies is nectar on which these insects feed, and pollen transfer is passive. Sugar concentration is normally somewhat lower than in other insect pollination systems (Johnson & Bond, 1994; Goldblatt & Manning, 1998), mostly 18–24% sucrose equivalents, but volume is high and sugars are typically sucrose-rich to -dominant. The exceptions are *G. cruentus* and *G. saundersii*, which have hexose-rich to hexose-dominant nectar (Goldblatt & Manning, 2002).

Some 9 species, 5% of the southern African species, may be inferred as being adapted for *Aeropetes* pollination (Table 3). Species belong to three sections (*Blandus*: 5 spp., *Linearifolius*: 2 sp., and *Ophiolyza*: 2 spp.—Table 4). Thus, we hypothesize the origin of the strategy a minimum of three times. Except in series *Linearifolius*, floral morphology of *Aeropetes* pollinated flowers is remarkably similar and is associated with large flowers with spreading tepals and white splashes on the lower tepals. In section *Linearifolius*, *G. nerineoides* has relatively small flowers, but several flowers are usually open at the same time, providing the display comparable to one large flower found in sections *Ophiolyza* and *Blandus*.

7. Hopliine beetles. These beetles of the family Scarabaeidae use the flowers of a range of plant families for sites of assembly, mate selection, and copulation (Steiner, 1998; Goldblatt et al., 1998b) and sometimes consume pollen or other plant materials. Flowers most commonly favored by these beetles are salver- or bowl-shaped, actinomorphic, and although variously colored, typically have dark contrasting markings, sometimes called beetle marks (painted bowl flowers of Bernhardt, 2000). The only *Gladiolus* species that approaches this pattern is *G. meliusculus*, which has pink flowers with enlarged lower tepals that form a comparatively large platform. The lower tepals have a broad, dark transverse band and are yellow at the tips. The pigmentation broadly mimics that of two species of *Romulea* (Iridaceae) that often grow sympatrically and are visited by the same beetle species. However, *G. meliusculus* has a zygomorphic flower that produces a floral odor and a short perianth tube containing measurable amounts of nectar, and it is also visited by *Andrena* sp., a short-tongued bee. Too few visits by bees were observed for us to assess their importance in the pollination of this species. It is possible that the bee is at best an occasional visitor, unlike the beetles, which could consistently be found on flowers of these species at our study sites. The floral form of *G. meliusculus* suggests a recent shift to hopliine pollination, and it does not have the classic appearance associated with species pollinated by hopliines.

DISCUSSION

Much of the evolutionary radiation in Iridaceae has involved changes in floral features, and it comes as no surprise that floral morphology in the family is closely correlated with pollination strategy. These are often very precise and involve a narrow range of pollinators, often a single pollinator group or only one pollinator (Table 2). The seven taxonomic sections of *Gladiolus* (Table 4) recognized in southern Africa by Goldblatt and Manning are each considered to be monophyletic, as are their constituent series (Goldblatt & Manning, 1998), and they are defined by unique, derived characters.

NECTAR

Two surprising results have emerged from an analysis of nectars produced by *Gladiolus* flowers (Johnson & Bond, 1994; Goldblatt et al., 1998a, 1999; Goldblatt & Manning, 1999, unpublished data). Irrespective of taxonomic affinity and, with two exceptions, of pollinator, nectars are sucrose-rich to sucrose-dominant. The exceptions are a lineage of three bird pollinated species of section *Hebea*, *G. cunonius*, *G. saccatus*, and *G. splendens*, and two species of section *Ophiolyza* inferred to be butterfly pollinated, *G. cruentus* and *G. saundersii*, which have hexose-rich to hexose-dominant nectar. The development of hexose-rich nectar in section *Hebea* is consistent with the presumed taste preferences of passerine birds (Baker & Baker, 1990). However, comparable evolution of hexose-rich nectar is conspicuously absent in the four other sections of southern African *Gladiolus* that contain bird pollinated species. The development of hexose-rich nectar in section *Ophiolyza* is likewise noteworthy, as it is unusual for butterfly flowers in the Iridaceae (unpublished data), though not unique. *Hesperantha (Schizostylis) coccinea*, a presumed butterfly flower, has hexose-dominant nectar (Johnson & Bond, 1994) in contrast to the bee or moth pollinated members of that genus (Goldblatt et al., in press).

In general, nectar sugar chemistry in *Gladiolus* appears to reflect phylogenetic relationship rather than pollinator preference, as has been reported, for example, in African Asphodelaceae and Ericaceae (Percival, 1961; van Wyk et al., 1993; Barnes et al., 1995). However, natural selection by pollinators presumably accounts for the shift to hexose-rich nectar in section *Hebea* of *Gladiolus*. *Aeropetes* is, however, not known to have a preferred type of nectar, so the shift to hexose-rich nectar in butterfly pollinated species of section *Ophiolyza* is puzzling.

Nectar concentration seems to be loosely linked to pollinator (Kevan & Baker, 1983; Baker & Baker, 1990), and this is to a limited extent reflected in *Gladiolus*. Flowers of *Gladiolus* pollinated by apid-anthophorine bees or moths typically have relatively concentrated nectar, between 30% and 36% sucrose equivalents. Species pollinated by long-proboscid flies typically have slightly more dilute nectar, 20% to 30% (Goldblatt & Manning, 1999, 2000). Butterfly flowers have moderate sugar concentrations, in *Gladiolus* between 18% and 26%. The latter pattern is consistent with Johnson and Bond's (1994) observations on flowers pollinated by *Aeropetes*.

Flowers pollinated by nectarinids, however, show no apparent pattern in *Gladiolus*. Bird pollinated species of series *Homoglossum* have sugar concentrations ranging from 28% to 33%, but in series *Mutabilis* of the same section as low as 21–26% in *G. priorii* and 37% in *G. meridionalis*, the latter remarkable in bird pollinated flowers. In contrast, bird pollinated species of section *Ophiolyza* have nectar mostly of 18–20% concentration except for *G. flanaganii*, which has nectar of 35% concentration. This absence of pattern is likewise consistent with Johnson and Bond's (1994) observations on flowers pollinated by nectarinids. Avian nectar feeders tend to favor more dilute nectars (Kevan, 1984; Baker & Baker, 1990; Nicholson, 1998), and this is reflected in the nectar of many *Gladiolus* species. The high nectar concentration in the species of series *Homoglossum* and *G. meridionalis* may reflect heightened calorific requirements in sunbirds in the winter, when temperatures are low and breeding occurs. In wet winter conditions rain may also cause dilution of nectar (Nicholson, 1998), and the high nectar concentration in these *Gladiolus* species may, alternatively and simply, be an adaptation to counteract the dilution effect.

Nectar volume, as might be expected, is closely linked to pollinator size, itself linked to flower size (Baker & Baker, 1990). The larger the pollinator the larger the flower and the greater the amount of nectar. Thus bird flowers have the highest quantities of nectar, and bee (and hopliine) flowers the lowest. Butterfly and long-proboscid fly flowers fall between the extremes. Hopliine and small-bodied bee pollinated flowers either produce reduced amounts of nectar or none at all. *Gladiolus* flowers, then, appear to be excellent sources of nectar for the particular pollinator for which they are adapted and floral changes associated with shifts in pollination system are tracked by nectar volume and concentration. Nectar sugar chemistry seems more conservative and is largely sucrose-rich to -dominant as it is in most members of subfamily Crocoideae (syn. Ixioideae) (Goldblatt et al., 1995, 1999, 2000a, 2000b, in press; Manning & Goldblatt, 1996, 1997). The marked trend away from this pattern in one bird pollinated lineage of section *Hebea*, which has hexose-rich to hexose-dominant nectar, seems likely to be pollinator driven. This same pattern occurs in several bird pollinated lineages of the family, including *Klattia* and *Witsenia* (Nivenioideae) and *Chasmanthe* (Crocoideae), but not in others (Goldblatt, 1993; Johnson & Bond, 1994; Goldblatt et al., 1999).

POLLINATOR SHIFTS AND EVOLUTION IN THE GENUS

In their analysis of the radiation of pollination systems in *Disa* (Orchidaceae) in southern Africa, Johnson et al. (1998) asked two questions. One, did each system originate once or did each mode have several independent origins? Two, does history play an important role in determining the pollination biology of a species or are pollination systems evolutionarily labile? These questions can equally be asked of *Gladiolus*, and the answers are strikingly similar. As in *Disa*, there is ample evidence from comparative morphology and cladistic analysis that different pollination systems arose repeatedly within *Gladiolus*. Thus, we conclude that, within certain parameters, pollination systems in the genus are extremely labile. There is always a historical component to the radiation of pollination systems, and the zygomorphic, tubular, often large, nectar-producing flowers of *Gladiolus* seem constrained to utilizing pollination systems that involve passive pollen transfer with pollinators visiting flowers in search of nectar. This contrasts markedly with genera like *Hesperantha*, *Ixia*, and *Romulea*, which have small, rotate, or campanulate flowers that emphasize pollination systems involving hopliine beetles or bees foraging for pollen, or a combination of hopliines and bees. Thus, hopliine beetles, which favor actinomorphic, salverform flowers; butterflies, other than *Aeropetes*; bombyliid flies, which favor relatively small flowers; and carrion flies; all significant pollinators of the southern African flora, are not at all or are or barely utilized within *Gladiolus*. Even the active pollination system involving female bees foraging for pollen is weakly developed, although it has evolved independently in four species of four different sections or series (*G. aureus*, *G. brevitubus*, *G. quadrangulus*, and *G. stellatus*).

It has been implicitly assumed that explicit phylogenetic hypotheses based on well-supported cladistic analyses are necessary to determine patterns of floral radiation and associated diversity of pollination systems in flowering plants (Armbruster, 1992, 1993; Johnson et al., 1998). We lack such a phylogeny in *Gladiolus*, but the monographs of the genus for tropical and southern Africa offer phylogenetic classifications and preliminary cladograms based on morphological analysis (Goldblatt, 1996, Goldblatt & Manning, 1998). In southern Africa, Goldblatt and Manning recognize seven sections in the genus (Table 4), each supported by specialized features (synapomorphies). Within these sections a total of 21 species aggregates (informal taxonomic series) are also recognized, these likewise supported by derived characters. Thus, a phylogenetic framework exists, which offers a broad understanding of the major patterns of radiation in the genus. Pollination biology in *Gladiolus* is also moderately well understood. Pollination by anthophorine bees and native *Apis mellifera* foraging for nectar and passively transporting dorsal loads of pollen is the most common system, now documented in 43 species. The close similarity of floral morphology and nectar characteristics suggest that an additional 44 species share this same pollination system (Table 3).

Pollination systems in *Gladiolus*, in order of importance (Table 3) then, are large-bodied, long-tongued bees (53%), long-proboscid flies with probosces over 20 mm long (18%), nectarinid birds (12%), night-flying moths (7%), the satyrid butterfly, *Aeropetes* (5%), and small-bodied, short-tongued female bees foraging for pollen (2%). The common hopliine beetle system of southern African Iridaceae is represented in just one species. Matching the pollination strategy against the classification of the genus shows repeated shifts in pollination system (Table 4). Assuming that large-bodied, long-tongued bee pollination is ancestral, as postulated above, we suggest a minimum estimate of the independent origin of long-proboscid fly pollination at least 12 times (in six sections of the genus). Likewise, we infer the independent origin of passerine pollination 7 times (in 7 series in four sections), moth pollination 5 times (in 5 series in 3 sections), and *Aeropetes* pollination 3 times (in 3 series in 3 sections). Combining this with the independent origin of active bee pollination in four species in four separate series and hopliine pollination in one series, we infer a total of at least 32 shifts in pollination system within *Gladiolus*. Put another way, this represents one shift for every 5 species of *Gladiolus*. This appears to be a remarkable degree of flexibility in floral characters and in patterns of convergent evolution, at least as far as current knowledge allows this statement.

PATTERNS OF SPECIATION—GEOGRAPHY VERSUS POLLINATION SYSTEM

A more difficult question to answer than the frequency of pollinator shifts is why these shifts occurred. Two factors appear significant in pollinator shifts in *Gladiolus*. One frequent pattern is an associated shift in soil substrate without any significant geographic disjunction among closely related species with different pollinators. Several examples illustrate this point. In the four species of series *Floribundus*, bee pollinated *G. rudis* and *G. grandiflorus* grow on sandstone or clay slopes respectively, fly pollinated *G. floribundus* on drier rocky sandstone habitats, and bird pollinated *G. miniatus* is restricted to coastal limestones. In series *Permeabilis*, *G. permeabilis* subsp. *edulis* favors sandy or rocky doleritic-derived soils, whereas the immediately related *G. sekukuniensis* is restricted to dolomite and other limestone-type soils (Manning et al., 1999). In the three species of series *Appendiculatus*, bee pollinated *G. appendiculatus* occurs on igneous substrates, while the two fly pollinated species, *G. calcaratus* and *G. macneilii*, occur on sandstone- or dolomite-derived soils, respectively. A similar pattern is mirrored in series *Gracilis*, where moth pollinated *G. maculatus* favors clay soils, while the closely related *G. priorii* and *G. meridionalis*, both bird pollinated, favor rocky sandstone or granite slopes (*G. priorii*) or coastal limestones (*G. meridionalis*). As in *Lapeirousia* (Goldblatt & Manning, 1996), one pattern of species diversification in *Gladiolus* is marked by an edaphic shift accompanied by a change in pollinator without a marked geographic disjunction.

A second pattern of speciation is associated with a shift in flowering phenology. In the southern African winter-rainfall zone this shift is sometimes combined with a change in pollinator in closely related species. A phenological shift is consistently associated with *Aeropetes* pollination because this butterfly is on the wing from late December to April. At least three clades comprise species that flower in the late summer or autumn and show a shift to *Aeropetes* pollination. This phenological shift need not accompany a change in pollinator. Several autumn-flowering species of sections *Homoglossum* and *Linearifolius* maintain ancestral large-bodied anthophorine bee pollination but flower at a time when few other members of the surrounding flora are in bloom, and competition for bee pollination must be minimal. In the winter-rainfall zone, related species flower at the expected time, earlier in the season. In the summer-rainfall zone there is a comparable phenological shift in species of section *Linearifolius*, in this case for flowering earlier in the season, at the end of the dry season and before the flowering peak in the flora. Phenological shifts, whether accompanied by pollinator shifts or not, are generally accompanied by changes in patterns of vegetative growth (Goldblatt & Manning, 1998). Most often the production of leaves is delayed until conditions are favorable for vegetative growth, and leaves present at flowering time are reduced in size and often in number. Alternatively, the flowering stem with its reduced leaves does not die as the seeds mature, but remains green throughout the growing season.

Long-proboscid flies are on the wing late in the flowering season, mainly October to December in the winter-rainfall zone, February to April in the summer-rainfall zone. Shifts to this pollination system may be driven by selection by these insects. An aspect of pollination by extreme specialists, either long-proboscid flies or *Aeropetes*, that awaits explanation is the prominence of these systems as soon as these insects are on the wing. Bees are the predominant pollinators in the winter-rainfall zone early in the season (late winter and spring) and in the late spring and early summer in the summer-rainfall zone, but their importance for genera like *Gladiolus* falls dramatically once long-proboscid flies and then *Aeropetes* become active. It may be that competition for conventional pollinators (apid-anthophorine bees) influences the shift to specialist pollinators. There is, however, no evidence that bee populations also fall at this time, which might lead to the exploitation of alternative pollinators. It may simply be that long-proboscid flies, which usually carry pure loads of pollen of particular species at various sites on their bodies (Goldblatt & Manning, 1999, 2000) are more effective pollinators. Bees remain active and plentiful in the summer-rainfall zone thoughout the time that long-proboscid flies and *Aeropetes* are active. In the winter-rainfall zone apid bees also remain active and prominent pollinators of *Gladiolus* species that flower in late summer and autumn.

As noted for subgenus *Lapeirousia* in winter-rainfall southern Africa (Goldblatt & Manning, 1996), edaphic shifts appear to be the primary step in population differentiation, which is then reinforced by a pollinator shift. This may be more readily accomplished in small peripheral populations separated ecologically from the swamping effects of the ancestral gene pool. The second pattern, which involves a phenological shift, may be entirely pollinator driven. Whatever the full explanation may be, there is no doubt that pollinator shifts explain much of the species diversity in the African genera of the Iridaceae.

Species diversification within the same pollination system requires different explanations. Some species fit the classic pattern of divergence caused by geographic isolation alone. For example, within series *Homoglossum* the lineage of similar-flowered, bird pollinated species, *G. quadrangularis*, *G. teretifolius*, and *G. watsonius*, occupy separate, although adjacent geographic ranges, but maintain identical soil preferences, flowering times, and pollinators (Goldblatt & Manning, 1998). A comparable pattern is evident in the second lineage of the series, in which *G. abbreviatus*, *G. fourcadei*, and *G. huttonii* have adjacent ranges across the southern and eastern Cape, but there is a shift in phenology in *G. abbreviatus* to winter-flowering as compared to its spring-flowering relatives.

Speciation patterns are often more complex. Competition for the same suite of pollinators at times of flowering peaks, August and September in the winter-rainfall zone and December to February in the summer-rainfall zone, is one explanation for the presence of species clusters in sections *Densiflorus*, *Hebea*, and *Homoglossum*, all pollinated by the same range of large-bodied bees. Under intense competition for pollinators, a distinctive display of form, color, or even fragrance may enhance reproductive success. In a genus such as *Gladiolus*, where species are self-incompatible but are almost all interfertile, only highly distinctive species sharing the same pollinator can coexist in a particular habitat, whatever their edaphic niche may be, without the development of hybrids. It is not unusual to find three or four coblooming species of *Gladiolus* sharing the same set of bee species as their pollinators. Each *Gladiolus* species has its own microhabitat, so that competition for space and nutrients is not a concern. However, in such situations species invariably differ substantially in appearance and fragrance. Anthophorine bees, which are to a degree flower constant (Bernhardt, 1996; Goldblatt et al., 1998b), do not visit these different species sequentially, and hybridization is rare in our experience, and unknown in undisturbed habitats. We therefore assume that introgression is not an explanation for much if any of the species diversity in the genus. Reproductive isolation due to polyploidy or dysploidy can also be largely ruled out as having played a role in the radiation in southern African *Gladiolus*. Nearly all species are diploid and have the same chromosome number, $n = 15$ (Goldblatt & Takei, 1997). Only *G. dalenii* is consistently polyploid in southern Africa (diploid races occur in tropical Africa and Madagascar), and *G. leptosiphon*, $n = 30$, may be a polyploid species, although only one population has been examined for chromosome number (Goldblatt et al., 1993; Goldblatt & Takei, 1997). The predominant factors that promote reproductive isolation in *Gladiolus* then are floral presentation frequently combined with edaphic or phenological shifts, phenological shifts alone, or conventional geographic barriers to dispersal.

SPECIALIST POLLINATION SYSTEMS AND RARITY

As pointed out by Johnson and Bond (1994) for species pollinated by *Aeropetes*, many of the plants are rare or have narrow ranges. This is certainly true of butterfly pollinated species of the winter-rainfall zone, but it is also true that these species are usually restricted to rare habitats that remain moist during the dry summer and autumn (Goldblatt & Manning, 1998). Long-proboscid fly pollinated species of the winter-rainfall zone also flower fairly late and require mesic habitats that limit their distribution. Thus the rarity or narrow ranges of species using specialist pollinators may be no more than a reflection of the scarcity of suitable habitats available to them compounded by the difficulty of dispersal to isolated habitats where they can become established. The correlation of specialist pollinator and rarity is misleading. It is probably not the result of the unusual pollination system but of the paucity of suitable habitats and the difficulty of dispersal to similar habitats, located considerable distances away.

In the southern African summer-rainfall zone some *Gladiolus* species are certainly rare. While the immediately related *G. permeabilis* is widespread across southern Africa, *G. sekukuniensis* is restricted to a narrow stretch of Northern Province. Similarly, *G. macneilii* is a narrow endemic, whereas allied and presumably ancestral *G. appendiculatus* has a far wider range. However, both these rare species are also edaphic specialists, confined to unusual limestone soils. The correlation here, then, is a reflection of edaphic shift being associated with a change in pollinator.

CONCLUSION

The ultimate explanation for the success of *Gladiolus* compared to related genera in the family seems to lie in a genetic system that allows for adaptation to many different habitats, soil types, and climatic conditions combined with an extremely labile floral form that is receptive to selection. If there is one feature of the reproductive system that appears distinctive in *Gladiolus* it is that most species appear, at least from preliminary studies (Goldblatt et al., 1998a; Goldblatt & Manning, 1999), to be self-incompatible, unlike other genera in the same subfamily, and moreover, the flowers are strongly protandrous and herkogamous, also unlike the situation in other Crocoideae (where this is known). The genus also has a high basic chromosome number, $x = 15$, one of the highest in the family. Outcrossing and associated genic recombination are therefore maximized. The only other genus that is comparable in the family, *Moraea* (subfamily Iridoideae), is also an unusually large genus with some 200 species, and it too shows strong self-incompatibility, protandry and herkogamy, but not a high basic chromosome number. Whatever the explanations may be for the species richness in *Gladiolus*, and they are probably numerous and complex, we can only marvel at the diversity and adaptability of this remarkable genus.

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