Evidence of bird pollination in Iridaceae of southern Africa

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ABSTRACT

Based on a characteristic floral presentation and sightings of sunbirds on many flowers with similar morphology, 64 species of Iridaceae in eight genera, *Babiana, Chasmanthe, Crocosmia, Gladiolus, Tritoniopsis, Watsonia* (subfamily Ixioideae), *Klattia*, and *Witsenia* (Nivenioideae), are inferred to be pollinated by five sunbird species (*Nectarinia*: Nectarinidae) in southern Africa. In Ixioideae bird flowers are typified primarily by red to orange colors, gullet or flag forms with elongate floral tubes mostly 30 to 60 mm in length, and exserted unilateral stamens. In Nivenioideae flowers are tubular (*Witsenia*) with included stamens and green and yellow in color, or a head-like inflorescence of small, actinomorphic flowers is tightly enclosed in large, leafy bracts that form a nectar reservoir. All bird pollinated species secrete fairly large quantities of nectar, but its volume, the concentration of dissolved sugars and the sucrose to hexose ratio vary both between and within genera. Elsewhere in the family bird pollination is infered for several species of *Gladiolus* in tropical Africa and Arabia and in four species of *Tigridia* (Iridoideae) in Mexico–Central America. Sucrose-rich to sucrose-dominant nectar is characteristic of flowers of subfamily Ixioideae but a few bird-pollinated Ixioideae have hexose-dominant nectar, the only type of nectar in Nivenioideae. It is argued that bird pollination predominates Ixioid taxa because this is the largest subfamily and the ancestral condition is a flower with a perianth tube and bilabiate, zygomorphic perianth which preadapts them for pollen dispersal by specialized passerines.

KEY WORDS
pollination,
sunbirds,
Iridaceae,
adaptive radiation.

RÉSUMÉ

Mise en évidence de la pollinisation par les oiseaux chez les Iridaceae d'Afrique australe.

L'aspect caractéristique de 64 espèces d'Iridaceae de morphologie florale similaire, ainsi que l'observation d'un grand nombre d'oiseaux, suggèrent qu'en Afrique australe, la pollinisation s'effectue grâce à cinq espèces de souimangas (*Nectarinia*: Nectarinidae) dans huit genres d'Iridaceae subfam. Ixioideae (*Babiana, Chasmanthe, Crocosmia, Gladiolus, Tritoniopsis, Watsonia*) et subfam. Nivenioideae *Klattia* et *Witsenia*. Chez les Ixioideae les fleurs de couleur rouge à orange, le périanthe à tube floral généralement très long (30-60 mm) et les étamines unilatérales exsertes caractérisent les fleurs susceptibles d'attirer les oiseaux. Chez les Nivenioideae les fleurs vertes ou jaunes sont tubulaires (*Witsenia*), à étamines incluses, ou l'inflorescence en capitule est composée de petites fleurs actinomorphes enveloppées dans de grandes bractées foliaires formant une poche nectarifère. Toutes les espèces pollinisées par les oiseaux sécrètent d'assez grandes quantités de nectar dont le volume, la concentration de sucres dissous et le rapport sucrose/hexose varient entre et à l'intérieur des genres. La pollinisation par les oiseaux dans d'autres membres de la famille est suggérée pour plusieurs espèces de *Gladiolus* d'Afrique tropicale et d'Arabie, ainsi que pour quatre espèces de *Tigridia* (Iridoideae) du Mexique et d'Amérique centrale. Du nectar riche ou dominant en sucrose caractérise les fleurs des Ixioideae mais quelques espèces de cette sous-famille, pollinisées par les oiseaux, produisent un nectar à hexose dominant, le seul type connu chez les Nivenioideae. La pollinisation par les oiseaux semble prédominer chez les Ixioideae car c'est la plus importante des sous-familles, et ses membres possèdent des fleurs tubulaires et bilabiées (caractères ancestraux) qui les préadaptent à la pollinisation par des passereaux spécialisés.

MOTS CLÉS
pollinisation,
souimangas,
Iridaceae,
radiation adaptative.

INTRODUCTION

Bird pollination remains one of the most easily recognized pollination systems in the angiosperms. Regardless of whether the dominant pollinators are hummingbirds (Trochilidae), lorikeets (Loridae), or several families of passerines (e.g., Meliphagidae, Nectarinidae) bird pollination is easily recognized in flowers sharing a suite of three uniting characteristics. First, flowers lack detectable odor; second, red-orange pigmentation usually predominates (although other, contrasting colors occur); third, floral organs are usually reinforced with external layers of cutin and/or additional internal, fibers and xylem strands (GRANT & GRANT 1968; FAEGRI & VAN DER PIJL 1979; BERNHARDT & KNOX 1983).

The literature on bird pollination in dicotyledons has long exceeded that on the monocots. However, general ecological studies suggest that bird pollination has evolved repeatedly in petaloid monocots in regions where birds comprise a consistent portion of the nectarivore fauna (GRANT & GRANT 1965; FORD & PATON 1977; FEINSINGER & COLWELL 1978; PYKE 1980; REBELO 1987). Available evidence suggests that bird pollination in petaloid monocots converges with the evolution of bird pollination in dicot lineages.

There are two recurrent patterns in the evolution of bird pollination in monocotyledons. First, bird pollination occasionally represents a dominant strategy in a lineage. That is, morphological and biochemical characters show early adaptive radiation toward ornithophily and sys-

tematists often use these characteristics to delineate genera. For example, bird-pollinated *Anigozanthos* (Haemodoraceae) is separated from insect pollinated *Conostylis* (HOPPER & BURBIDGE 1978) largely by those features that represent adaptations for bird pollination. Bird pollination appears to be a dominant evolutionary trend in most lineages within Zingiberales (KRESS 1990). The second, more common pattern is that bird pollination is a recurrent, but recently derived, shift in largely insect-pollinated lineages. For example, there are a few species of *Fritillaria* and *Lilium* (Liliaceae) pollinated by hummingbirds in western North America (GRANT & GRANT 1968).

Field observations (SCOTT ELLIOT 1890; MARLOTH 1901, 1917–1932; VOGEL 1954; GOLDBLATT 1989, 1993) combined with some nectar analyses (I. BAKER in GOLDBLATT 1989, 1993) indicate that both evolutionary patterns occur within the Iridaceae in southern Africa. This is to be anticipated for two reasons. First, there are 20 species of nectarivorous sunbirds (Nectarinidae) in southern Africa (SKEAD 1967). Second, southern Africa is the center of diversity for the family Iridaceae (GOLDBLATT 1991), and research has shown that adaptive radiation of pollination systems is common in the family within and between genera (GOLDBLATT et al. 1995, 1998a, 1998b; GOLDBLATT & MANNING 1998). Reviewing the earlier literature, REBELO (1987) identified bird pollination in six families of petaloid monocots including the Iridaceae. VOGEL (1954) found evidence for bird pollination in 13 genera of Iridaceae native to southern Africa (now reclassified into just 6 genera): *Anaclanthe* (= *Babiana*), *Anapalina* (= *Tritoniopsis*), *Anomalesia* (= *Gladiolus*), *Antholyza* (= *Babiana*), *Chasmanthe*, *Curtonus* (= *Crocosmia*), *Homoglossum* (= *Gladiolus*), *Kentrosiphon* (= *Gladiolus*), *Petamenes* (= *Gladiolus*), *Watsonia*, and *Witsenia* (current generic names in parentheses). VOGEL's study and more recent work of GOLDBLATT (1989, 1993) indicate that bird pollination has evolved more frequently within subfamily Ixioideae than in subfamily Nivenioideae and is not represented in African members of subfamily Iridoideae (family classification following GOLDBLATT 1990a).

Analyses of bird pollination in the Iridaceae remains fragmentary and largely anecdotal. Nevertheless, circumstantial evidence clearly indicates that this pollination system appears to have evolved in many lineages within the African Iridaceae. We present additional data based on field observations and biochemical analyses to better document the strategy and identify characters that may be used to construct future phylogenies.

MATERIALS AND METHODS

FIELD OBSERVATIONS.—Observations represent approximately 120 hours in the field from 1986 to 1997 (Table 1). Identification of avian floral foragers follows MACLEAN (1985). Additional observations of the satyrid butterfly, *Aeropetes tulbaghia*, were made without collecting vouchers as this large insect is immediately recognizable and cannot be confused with any other diurnal lepidopteran in southern Africa (VAN SON 1955). Observations were confined to daylight hours when sunbirds are active. No birds were captured and we therefore have no information on pollen carried by sunbirds.

FLORAL MEASUREMENTS.—Perianths of fresh flowers were measured in situ and from botanical garden collections. Measurements of the perianth tube length are made from the base of the tube to the point at which the tepals separate from the tube.

SCENT DETECTION.—Flowers of all species observed were smelled in situ and in greenhouse plants grown at the Missouri Botanical Garden.

NECTAR.—Nectar samples were extracted from flowers using 3 μl microcapillary tubes. Removal of the entire fluid contents of a singe flower often required using the same microcapillary tube repeatedly. Nectar was extracted from flowers as outlined by GOLDBLATT et al. (1995, 1998b). The percentage of sucrose equivalents in fresh nectar was measured in the field or laboratory on a Bellingham and Stanley hand-held refractometer (0–50%). Flowers of 10 individuals per population were sampled, unless fewer individuals were available. Additional nectar samples were dried on Whatman's filter paper no. 1 and sent to the late Irene BAKER, University

TABLE 1.—Records of sunbird visits in species of Iridaceae where birds have been observed to probe flowers for nectar and brush against anthers and stigmas. Records are original unless referenced. Numbers in parentheses are number of species inferred to be bird pollination of the total in the genus. No other potential pollinators were noted during our observations of these species except as noted in column 3.

Taxon	Sunbird	Record data
Ixioideae		
Babiana (3/65)		
B. ringens	*N. famosa*	W. Cape, Yzerfontein, Sep. 1991
B. thunbergii	*N. fusca*	W. Cape, Lambert's Bay, Sep. 1995
	N. famosa	N. Cape, Hondeklipbaai, Aug. 1998 (C. PATERSON-JONES, pers. comm.)
Chasmanthe (3/3)		
C. aethiopica	*N. chalybea*	(SCOTT ELLIOT, 1890-no locality details); W. Cape, Table Mountain, July (VOGEL 1954); W. Cape, Kirstenbosch, July 1994
	N. famosa	W. Cape, Voelvlei, Bredasdorp, June 1995
C. floribunda	*N. chalybea*	W. Cape, Saldanha Hills, Aug. 1995; Vredenburg, 27 July 1998; Langebaan Hill, 23 Aug. 1998
Crocosmia (3/7)		
C. paniculata	*N. afra*	Kwazulu-Natal, Tendele, Jan. 1991
	N. afra	Mpumalanga, Graskop, Feb. 1995
C. pearsii	*N. famosa*	Free State, near The Sentinel, Feb. 1995
Gladiolus (ca. 20/163)		
G. abbreviatus	*N. famosa*	W. Cape, Voelvlei, Bredasdorp, June 1995; near Hermanus, Aug. 1995 (FERREIRA, pers. comm.)
G. cunonius	*N. chalybea*	W. Cape, Strandfontein, Cape Flats, Oct. 1996
G. dalenii	*N. afra*	Kwazulu-Natal, Mahai Valley, without date (VOGEL 1954)
	N. famosa	Kwazulu-Natal, Witzieshoek, Feb. 1997.
G. flanaganii	*N. famosa*	Kwazulu-Natal, Sani Pass, Jan. (O.M. HILLIARD, pers. comm.)
G. meridionalis	*N. violacea*	W. Cape, near Pearly Beach, July 1995.
G. saccatus	*N. fusca*	N. Cape, S. Namaqualand, Sep. 1995
Tritoniopsis (ca. 7/22)		
T. caffra	*N. chalybea*	W. Cape, George, Mar. 1998.
T. pulchra	*N. violacea*	W. Cape, Pearly Beach, July 1995;
	N. chalybea	S. of Elim, May 1996
T. triticea	*N. violacea*	W. Cape, Glencairn, Mar. 1997 (plants also visited by *Aeropetes* there and often seen elsewhere)
T. williamsiana	*N. violacea*	W. Cape, Vogelgat, Hermanus, Jan. 1988 (GOLDBLATT 1990); Feb. 1997
Watsonia (24/52)		
W. angusta	*N. violacea*	W. Cape, Swellendam, Oct. 1986
W. meriana	*N. violacea*	W. Cape, Langebaan, Sep. 1995
W. schlechteri	*N. famosa*	W. Cape, Nuweberg, Jan. 1986 (GOLDBLATT 1989); Vogelgat, Hermanus, Feb. 1997 (N. HANEKOM & I. NÄNNI, pers. comm.)
W. stokoei	*N. violacea*	W. Cape, Suurvlakte, Grootwinterhoek Mts., Nov. 1995
W. tabularis	*N. violacea* (also robbing nectar)	W. Cape, Kalk Bay, Nov. 1985 (GOLDBLATT 1986)
	N. famosa (with *N. violacea* robbing nectar)	W. Cape, Silvermine, Nov. (PATERSON-JONES, pers. comm.)
	N. famosa	W. Cape, Table Mt., lower plateau, Dec. (STEINER, pers. comm.)
Nivenioideae		
Klattia (3/3)		
K. flava	*N. violacea*	W. Cape, Nuweberg, Nov. 1991 (GOLDBLATT 1993)
K. stokoei	*N. violacea*	W. Cape, Kogelberg, Nov. (REBELO 1987 & pers. comm.)
Witsenia (1/1)		
W. maura	*N. famosa*	W. Cape, Betty's Bay, Mar. 1990 (GOLDBLATT 1993)

of California, Berkeley or B.-E. VAN WYK, Rand Afrikaans University, Johannesburg, for HPTLC sugar analysis.

RESULTS

AVIAN FORAGING AND FLORAL PHENOLOGY

A total of five *Nectarinia* species were observed foraging on the flowers of 24 species in 8 genera of southern African Iridaceae (Table 1). Genera visited by sunbirds fall into two subfamilies: Ixioideae (*Babiana*, *Chasmanthe*, *Crocosmia*, *Gladiolus*, *Tritoniopsis*, and *Watsonia*); and Nivenioideae (*Klattia* and *Witsenia*). Based on floral morphology, an additional 38–40 species in these genera may be inferred to have flowers adapted for pollination by sunbirds. Floral morphology indicates that bird pollination is not represented in other genera of African Iridaceae. We have no observations of Iridaceae visited by native *Zosterops* species (Zosteropidae).

Iridaceous taxa visited by sunbirds (including those inferred to have bird flowers) may be found in flower from almost throughout the year (Fig. 1). However, the patterns in the two op-
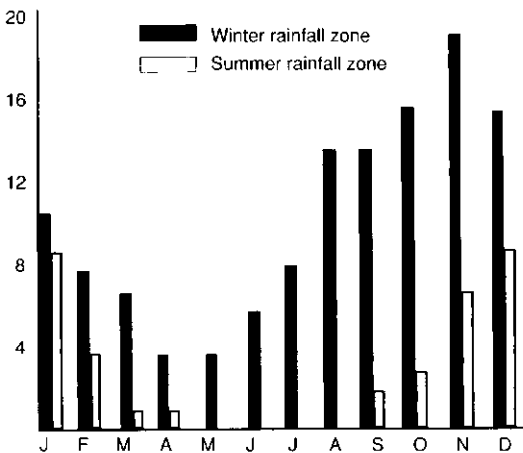

Fig. 1.—Floral seasonality of bird pollinated species of **Iridaceae** in southern Africa, contrasting flowering of species of the summer- and winter-rainfall zones of the subcontinent. In the summer-rainfall zone flowering peaks in the summer months, December and January, and ceases in winter whereas flowering in the winter-rainfall zone occurs throughout the year, but is highest in the spring and early summer, August to December.

TABLE 2.—Bill length in African sunbirds (*Nectarinia*) observed visiting flowers of Iridaceae.

Species	Bill length (range mm)
N. afra	24–29
N. chalybea	18–23
N. fusca	18–22
N. famosa	29–34
N. violacea	29–34

posed climate zones of the subcontinent differ. Flowering in the southern African winter-rainfall zone in the southwest of the subcontinent peaks between October and December, but appreciable numbers of species flower from July through February. In the summer rainfall zone in the eastern half of the subcontinent the flowering peak for bird flowers is November to January, and in the cooler, late autumn and winter months there are no bird-pollinated species in bloom.

Both male and female sunbirds may forage for nectar on flowers of the same species displaying no obvious agonistic behavior between the sexes. Sunbirds foraged by perching, usually on the stem below a flower, but sometimes on the inflorescence above the open flower, and inserted their bill into the floral tube. Bills range from 18–34 mm, with the smallest bills in *N. chalybea* and *N. fusca*, and the longest in *N. famosa* and *N. violacea* (Table 2).

While some observers have recorded sunbirds hovering while foraging in flowers this was never observed on flowers of Iridaceae. Flowers are approached in one of two ways. In erect inflorescences with horizontally held flowers (e.g., *Chasmanthe spp.*, *Gladiolus*, *Tritoniopsis*, and *Watsonia*), a bird usually grasps the stem below a flower and inserts its bill into the tube. In doing so its head comes into contact with the anthers, held on unilateral filaments below the dorsal tepal, and the stigmas held in approximately the same position. In contrast, when stems are flexed and inflorescences are ascending or horizontal, flowers face outward or toward the spike apex (*Babiana*, *Crocosmia*, and *Chasmanthe aethiopica*). A bird typically grasps the spike axis below the open flower and as it inserts its bill into the

Fig. 2.—Bird pollinated flowers of subfamily Ixioideae using *Gladiolus* species as typical examples: **A**, *G. saccatus* (tube relatively short and lower tepals forming a spur); **B**, *G. cunonius* (lower tepals vestigial); **C**, *G. abbreviatus*; **D**, *G. aurantiacus* (tube elongate, the upper part long and cylindric); **E**, *G. flanaganii*; **F**, *G. watsonius*. (Drawn by John Manning).

flower its throat and neck come into contact with the unilateral anthers and style.

Nectarinia violacea foraged on *Watsonia tabularis* in two ways. These birds sometimes inserted their bills into the floral tube but they will also puncture the floral tube with their bills and rob flowers of their nectar. Foraging bouts of all *Nectarinia* species regularly included visits to numerous open flowers of several different individuals of a species at a site, indicating the potential for cross pollination.

FORAGING BEHAVIOR OF OTHER ANIMALS

The large satyrid butterfly, *Aeropetes tulbaghia* was also observed visiting flowers of *Tritoniopsis triticea*, *Watsonia marlothii*, and *W. tabularis*, and probing the floral tubes with its proboscis. During foraging this butterfly could be seen to contact dehisced anthers and stigmas. The butterfly was not seen to be attacked by sunbirds.

COMPARATIVE FLORAL PRESENTATION

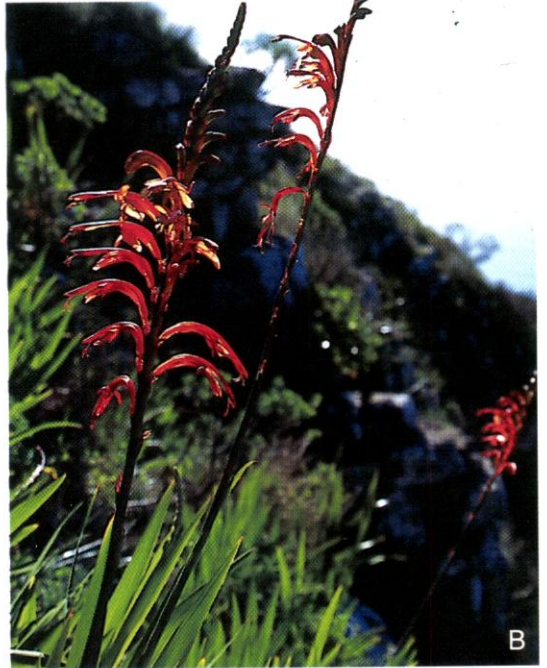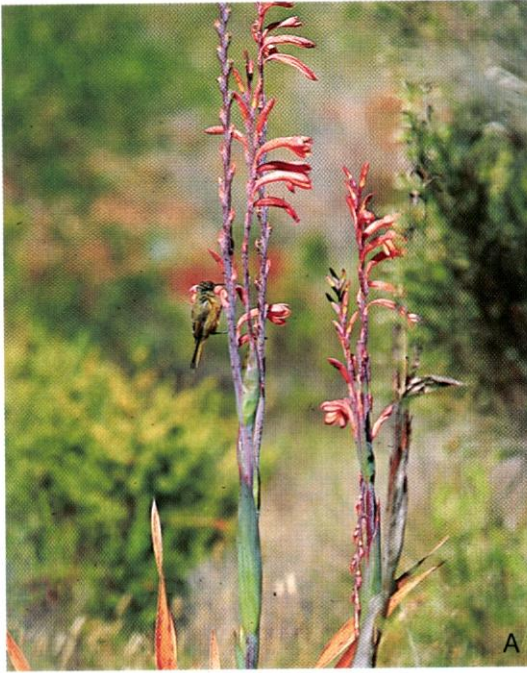While all bird pollinated Iridaceae have a floral

Fig. 3.—Bird pollinated species of **Iridaceae** subfamily Ixioideae: **A**, *Watsonia angusta*, with *Nectarinia famosa;* **B**, *Chasmanthe floribunda;* **C**, *Babiana ringens;* **D**, *Gladiolus watsonius.*

TABLE 3.—Floral characters in Iridaceae with bird flowers. Length of the wider, distal part of the tube is given only if there is a marked distinction between the proximal and distal parts of the tube, as is usual in species of subfamily Ixioideae.

Species	Flower		Tube length (mm)	
	color	form	total	wide part
IXIOIDEAE				
Babiana				
B. carminea Goldblatt & J.C. Manning, ined.	red	gullet	56–60	ca. 20
B. ringens (L.) Ker Gawl.	red	gullet	32–38	16–18
B. thunbergii Ker Gawl.	red	gullet	36–40	18–20
Chasmanthe				
C. aethiopica (L.) N.E. Br.	orange	gullet	30–40	23–28
C. bicolor (Gaspe ex Tenore) N.E. Br.	orange	gullet	40–50	30–38
C. floribunda (Salisb.) N.E. Br.	orange	gullet	30–33	ca. 24
Crocosmia				
C. paniculata (Klatt) Goldblatt	orange	gullet	25–46	15–23
C. pearsei Oberm.	orange	gullet	40–55	25–36
C. fucata (Herb.) M.P. de Vos	orange	gullet	ca. 45	ca. 25
Gladiolus				
sect. *Homoglossum*				
G. abbreviatus Andrews	red	gullet	40–52	14–26
G. fourcadei L. Bolus	red	gullet	35–46	24–26
G. huttonii (N.E. Br.) Goldblatt & M.P. de Vos	red	gullet	50–53	18–22
G. meridionalis G.J. Lewis	red/pink	gullet	40–48	22–24
G. priorii N.E. Br.	red	gullet	30–45	18–25
G. quadrangularis (Burm.f.) Ker Gawl.	red	gullet	43–55	30–32
G. teretifolius Goldblatt & M.P. de Vos	red	gullet	35–45	22–26
G. watsonius Thunb.	red	gullet	44–53	24–28
sect. *Hebea*				
G. cunonius (L.) Gaertn.	red	flag	12–15	ca. 3
G. saccatus (Klatt) Goldblatt & M.P. de Vos	red	flag	12–20	5–8
G. splendens (Sweet) Herbert	red	gullet	16–18	8–10
G. vandermerwei (L. Bolus) Goldblatt & M.P. de Vos	red	gullet	35–45	ca. 22
sect. *Linearifolius*				
G. overbergensis Goldblatt & M.P. de Vos	red	gullet	46–55	28–35
G. bonaspei Goldblatt & M.P. de Vos	orange (or yellow)	gullet	35–43	ca. 25
sect. *Ophiolyza*				
G. aurantiacus Klatt	orange	gullet	44–65	24–28
G. antholyzoides Baker	orange or yellow	gullet	28–40	ca. 15
G. dalenii van Geel	orange	gullet	35–50	n/a
G. flanaganii Baker	red	gullet	35–45	n/a
G. magnificus (Harms) Goldblatt	red	gulle	25–30	n/a
Tritoniopsis				
T. antholyza (Lam.) Goldblatt	red	gullet	25–40	16–20
T. burchellii (N.E. Br.) Goldblatt	red	gullet	30–40	18–25
T. caffra (Ker Gawl. ex Baker) Goldblatt	red	gullet	20–30	13–20
T. intermedia (Baker) G.J. Lewis	pink	gullet	25–30	18–20
T. pulchra (Baker) Goldblatt	red	gullet	30–33	15–18
T. triticea (Burm.f.) Goldblatt	red	gullet	25–30	16–20
T. williamsiana Goldblatt	red	gullet	ca. 25	12–15
Watsonia				
W. angusta (L.) Ker Gawl.	red	gullet	35–44	20–22
W. fourcadei Mathews & L. Bolus	orange/red	gullet	40–55	22–26
W. gladioloides Schltr.	red	gullet	40–50	20–30
W. hysterantha Mathews & L. Bolus	red	gullet	38–45	ca. 25
W. latifolia Oberm.	dark red	gullet	35–45	18–24
W. marlothii L. Bolus	red	gullet	24–30	14–22
W. meriana (L.) Mill.	red/purple	gullet	42–50	20–25

Species	Flower		Tube length (mm)	
	color	form	total	wide part
W. pillansii L. Bolus	orange to scarlet	gullet	35–50	18–25
W. schlechteri L. Bolus	red	gullet	40–50	22–30
W. spectabilis L. Bolus	red	gullet	40–46	20–25
W. stokoei L. Bolus	red	gullet	24–35	12–20
W. tabularis Mathews & L. Bolus	red/pink	gullet	40–50	20–25
W. vandermerwei L. Bolus	red	gullet	45–50	ca. 25
W. zeyheri L. Bolus	scarlet	gullet	30–35	16–20
NIVENIOIDEAE				
Klattia				
K. flava (G.J. Lewis) Goldblatt	yellow	brush	4.5–6	n/a
K. partita Ker Gawl. ex Baker	navy blue	brush	3.3–4	n/a
K. stokoei L. Guthrie	red	brush	1.5–5	n/a
Witsenia				
W. maura Thunb.	yellow and green	tube	50–55	n/a

tube the length of the tube is extremely variable (Table 3). *Klattia* species have the shortest tubes, no more than 8 mm in length, while *Gladiolus* species of sections *Homoglossum* and *Ophiolyza* (Fig. 2C–F), and *Witsenia maura* (Fig. 4A) have the longest tubes, often exceeding 45 mm.

Flowers visited by sunbirds are of three types. Gullet flowers occur in all bird flowers of subfamily Ixioideae and have the following characteristics: red (scarlet to crimson) to deep orange color; an elongate perianth tube; long-exserted, unilateral stamens; large flowers (5–8 cm long), with the dorsal (adaxial) tepal largest (Fig. 2A–D). The dorsal tepals is either hooded (Fig. 3A–C), concealing the stamens, or erect and somewhat flag-like. The lower three tepals are typically smaller than the dorsal (Fig. 3B–C) and sometimes all five other tepals may be much reduced or vestigial (Fig. 3A). The lower three tepals rarely have contrasting color and flowers lack detectable odor. This stands in marked contrast to southern African species of some of the same genera (*Gladiolus, Tritoniopsis*) that are pollinated by bees or moths or long-proboscid flies, which have prominent nectar guides and usually strong floral odors (GOLDBLATT & MANNING 1998; GOLDBLATT et al. 1995, 1998b).

Most often the perianth tube consists of a slender, cylindric, more or less erect lower part and an abruptly expanded, also cylindric, horizontal upper part. Floral tubes in these species form a lock and key association with the bills of sunbirds, particularly those species that have the upper part of the tube abruptly widened into a cylindrical upper part (Table 3). In these species a bird's bill is readily accommodated by the upper part of the tube, but nectar, restricted to the lower part of the tube, is reached by the bird's more slender tongue. The dorsal tepal is often nearly horizontal while the remaining tepals spread outward from the base and are either patent, somewhat recurved, or reduced to vestigial and directed forward forming part of the nectar reservoir. The stamens, inserted at the base of the wide, upper part of the tube, are sturdy and exserted well beyond the mouth of the tube. The anthers are usually appressed to the dorsal tepals and extend almost to the tepal apex.

Floral form varies but gullet flowers are always borne on spikes (Fig. 2A–D). The spicate inflorescences are usually stiffly erect and sturdy. Flowers are borne on branched or unbranched stems either opposed in two ranks (*Chasmanthe, Crocosmia, Tritoniopsis, Watsonia*), or are secund on straight, unbranched stems (*Gladiolus* sect. *Homoglossum, Linearifolius,* and *Ophiolyza*), or secund on flexuose unbranched stems (*Gladiolus* sect. *Homoglossum*). In bird flowers of *Gladiolus* sect. *Hebea* the stems are thick and branched and the spikes strongly inflexed. In *Crocosmia* the stems are usually several-branched and like those of section *Hebea*, strongly flexed. In both of these taxa the spikes provide the perch and sunbirds
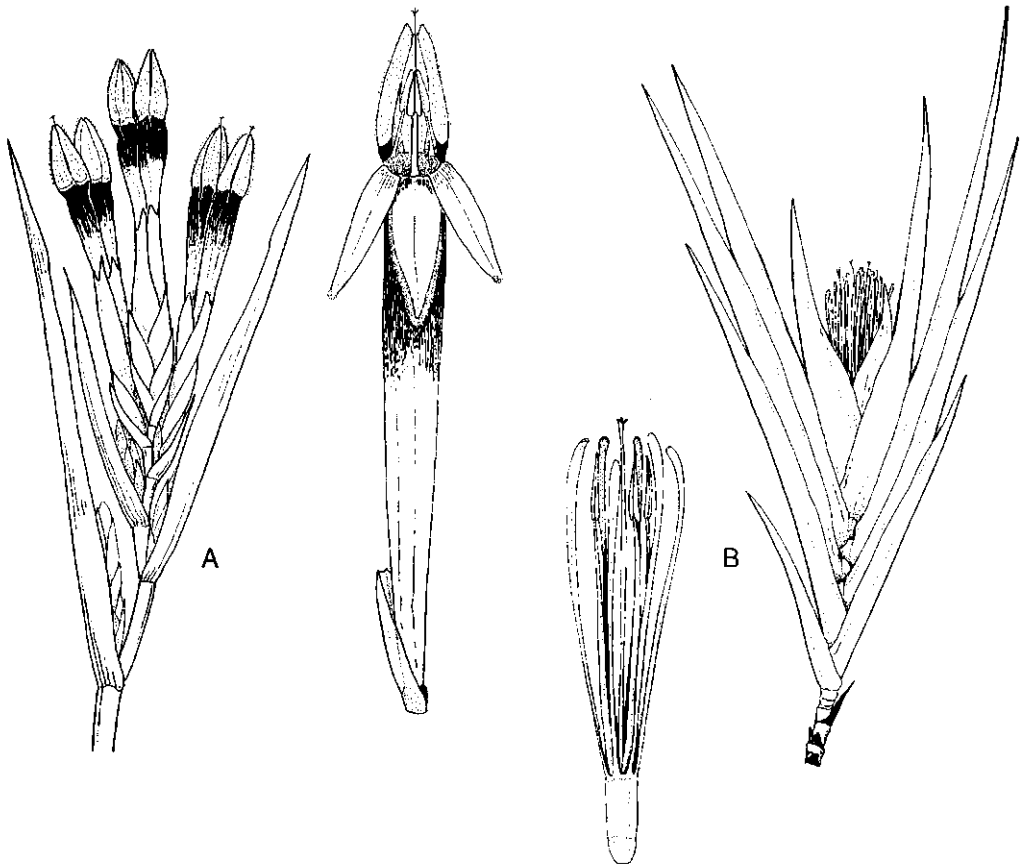
Fig. 4.—Inflorescence and individual flowers of bird pollinated examples of **Iridaceae** subfamily Nivenioideae: **A**, *Witsenia maura*: **B**, *Klattia flava*. Inflorescences full size, individual flowers × 2. (Drawn by Margo BRANCH).

approach these flowers from above, rather than from below as in conventional, erect spikes, in for example, *Gladiolus* and *Watsonia*. In *Babiana ringens* (Fig. 2D) the main branch of the flowering stem forms a sterile, sturdy perch, and short lateral branches bear the flowers in crowded spikes near ground level. In *B. thunbergii* the multibranched stems have horizontal spikes of crowded flowers. In both these *Babiana* species sunbirds grasp the erect stem or stand on the old flowers to probe for nectar in fresh, recently opened flowers.

Witsenia maura is the only putatively bird-pollinated species of Iridaceae with straight, tubular flowers (Fig. 4A). The floral tube is 50–55 mm long, 6 mm wide in the upper half, and the tepals are clasped together, the limbs

forming a cone that closes off the mouth of the tube. The stamens remain enclosed in the flower throughout anthesis but the style is exserted late in anthesis, then protruding through a small gap between the tops of the coherent tepals, presumably when it is receptive. The flowers are multicolored. The tube is deep green while the tepal claws are blackish and the limbs are bright yellow and densely felted externally. Nectar robbing is discouraged by two morphological adaptations. First, green leathery bracts enclose the lower (and nectar-containing) part of the tube. Second, the yellow tepal limbs are so tightly held together that they can only be separated by the thrust of a bird's bill (Fig. 4A detail). The flowers are borne on shortly branched, compound panicles

TABLE 4.—Nectar characteristics of flowers of Iridaceae adapted for sunbird pollination. Data for *Klattia* and *Witsenia* are from GOLDBLATT (1993), and for some *Watsonia* species from GOLDBLATT (1989). Most nectar sugar composition analyses were contributed by B.-E. VAN WYK; those contributed by I. BAKER or are taken from JOHNSON & BOND (1994) are indicted by superscript 1 or 2, respectively. Absence of data is indicated by – and (n) indicates the number of individuals sampled.

Species	Nectar		Range of sugars %			Sucrose
	volume l (n)	conc. % (±SD)	Fru	Glu	Suc	/F + G (n)
Babiana						
B. carminea	21–26 (3)	21.0 (2.6)	–	–	–	–
B. ringens	20–23 (2)	23.0 (–)	9	20	71	2.45 (1)
B. thunbergii	24–30 (10)	25.5 (0.8)	15–21	18–25	60–65	1.65 (4)
Chasmanthe						
C. aethiopica	24–30 (7)	15.7 (1.6)	43–45	40–42	14–15	0.17 (3)
	10.1 (6)	13.9 (–)	46	51	3	0.03 (1)[2]
C. floribunda						
(Kirstenbosch)	6.4–7.2 (3)	15.7 (0.3)	45–46	46–53	2–9	0.06 (3)
(Darling)	17–19 (2)	17.3 (–)	46	48	6	0.07 (1)
	15.7 (8)	16.8 (–)	45	46	9	0.10 (1)[2]
C. bicolor	11–12 (2)	10.0 (–)	45	52	3	0.03 (1)
Crocosmia						
C. fucata	9.8–12 (3)	18.0 (2.0)	20–34	28–40	26–52	0.51 (3)
Gladiolus						
G. abbreviatus						
(Napier road)	12–18 (4)	31.0 (2.7)	1–2	2–11	88–97	12.64 (3)
(Riviersonderend)	17–22 (8)	28.4 (0.8)	–	–	–	–
G. antholyzoides	15–21 (4)	20.0 (–)	12–13	18–20	67–70	2.18 (2)
G. aurantiacus	27–35 (5)	18.2 (1.6)	–	–	–	–
G. cunonius						
(Noordhoek)	14–19 (5)	18.6 (3.5)	27–29	33	38–40	0.64 (2)
(Blouberg)	22–27 (6)	21.8 (3.1)	23	29	46	0.88 (1)
G. dalenii	18 (1)	24.5 (–)	9	18	73	2.70 (1)
	16–24 (2)	20.0 (–)	–	–	–	–
G. flanaganii	27 (1)	35.0 (–)	8	12	80	4.00 (1)
G. meridionalis	15–20 (4)	33.4 (2.3)	–	–	–	–
G. miniatus	12 (1)	23.0 (–)	13	18	69	2.26 (1)
G. priorii	6.3–9.0 (5)	21.6 (4.0)	5	14	81	4.26 (1)
	13.4 (4)	26.3 (–)	6	13	81	4.26 (1)[2]
G. quadrangularis	20–33 (6)	30.8 (1.6)	–	–	–	–
G. saccatus	9.8–18 (5)	20.5 (1.1)	45–46	50–51	3–5	0.04 (2)
G. splendens	3.9–8.7 (3)	27.0 (1.0)	45–48	47–49	5–6	0.06 (2)
G. teretifolius	2.9–4.6 (5)	29.2 (1.1)	7	12	81	4.25 (1)
G. vandermerwei	30 (1)	20.0 (–)	10	12	78	3.55 (1)
G. watsonius	27–36 (3)	31.3 (2.6)	0–1	2	97–98	36.04 (3)
	15.6 (12)	27.9 (–)	1	2	97	32.33 (1)[2]
Tritoniopsis						
T. antholyza						
(Citrusdal)	5.4–6.6 (3)	16.1 (1.3)	19	23	58	1.4 (1)
(Grabouw)	14–20 (2)	27.5 (–)	3	9	88	7.2 (1)[1]
(Redhill)	4.7–6.9 (5)	25.8 (1.9)	2	6–7	90–93	10.76 (2)
T. burchellii	6.2 (9)	20.8 (–)	16	16	69	2.23 (1)[2]
T. caffra	2.8–6.8 (2)	25.0 (–)	21	21	58	1.38 (1)[1]
T. pulchra	3.7–11 (6)	26.3 (3.7)	4–6	4–7	87–92	7.63 (1)
T. triticea	3.6–6.8 (10)	20.5 (1.6)	9	10	81	4.26 (1)
	2.3 (7)	24.2 (–)	9	10	81	4.26 (1)[2]
T. williamsiana	6.2–7.9 (10)	24.2 (1.1)	–	–	–	–

Species	Nectar		Range of sugars %			Sucrose
	volume I (n)	conc. % (±SD)	Fru	Glu	Suc	/F + G (n)
Watsonia						
W. aletroides	14–16 (2)	23.8 (1.2)	52	20	**64**	1.74 (1)[1]
W. angusta	47–59 (5)	16.6 (0.5)	51–52	31–34	14–17	0.19 (2)[1]
W. fourcadei	51–85 (4)	17.8 (1.2)	23	21	56	1.28 (1)[1]
W. hysterantha	2.8–4.2 (3)	19.2 (1.6)	14–18	8–19	63–68	1.90 (2)
W. meriana						
(Kamieskroon)	24–55 (5)	20.9 (4.2)	28–39	20–27	35–50	0.78 (2)[1]
(Langebaan)	35–52 (2)	21.5 (–)	20–37	17–23	38–68	1.06 (2)
W. pillansii	35 (1)	18.0 (–)	21	26	**50**	1.06 (1)[1]
W. schlechteri	40–54 (2)	19.5 (–)	26	20	**53**	1.15 (1)[1]
W. stokoei	9.5–12 (10)	17.3 (1.5)	14–19	15–21	60–71	1.90 (2)
W. tabularis	45–70 (4)	17.5 (1.9)	15	17	69	2.22 (1)[1]
	25.6 (5)	14.5 (–)	17	21	62	* (1)[2]
W. vanderspuyiae	90–119 (5)	20.5 (2.6)	19	30	**51**	1.05 (1)[1]
Klattia						
K. flava	15–16 (2)	13.2 (–)	63	36	**1**	0.01 (1)[1]
K. partita	4.6–6.4 (2)	15.0 (–)	52	43	**6**	0.06 (1)[1]
K. stokoei	31–47 (4)	14.0 (2.3)	53–55	42–45	**1**	0.01 (2)[1]
Witsenia						
W. maura	65–78 (2)	12.0 (–)	42	53	**5**	0.06 (1)[1]
	27.8 (10)	13.5 (–)	45	55	**0**	0.0 (1)[2]

(GOLDBLATT 1993) carried at the top of sturdy, wand-like branches.

Brush flowers occur only in *Klattia* and the three species of this genus have flowers and inflorescences of similar construction. These small flowers are grouped in dense heads of 6–16 florets, forming a compound structure (GOLDBLATT 1993). Individual *Klattia* flowers consist of a short tube, linear-spathulate tepals, and elongate filaments and styles (Fig. 4B). Flowers are yellow in *K. flava*, dark navy blue in *K. partita*, and red in *K. stokoei*. Individual flower pairs are enclosed in membranous bracts and the entire head is tightly enveloped in opposed, enlarged leaves. These leaves are red in *K. stokoei* but green in the other two species. The entire inflorescence forms a brush-like unit. The inflorescences of *Klattia* species are borne on long sturdy erect branches that readily support the weight of sunbirds. The firm bracts enveloping the flower heads may discourage robbing and may provide a sturdy perch for sunbirds which probe the flowers through the top of the inflorescence.

Nectar presentation and analysis. In all species studied, nectar is secreted from septal nectaries

(GOLDBLATT & MANNING, unpubl.), and fluid is found within the tube by the time tepals first open. *Klattia* species were the only taxa studied in which nectar volume exceeds tube length, and nectar spills into the cavity created by the large enveloping spathes, often leaking between the spathe margins and becoming visible as a sticky exudate on their proximal surfaces.

Nectar volume per flower appears to be extremely variable and in some cases may be specific to genus and or species (Table 4). Based on our sampling of 41 species, there is no obvious correlation between the nectar volume and the concentration of dissolved sugars in bird-pollinated Iridaceae. For example, *Witsenia maura* obviously produced the greatest volume of nectar but sugar concentration is only about 12% whereas our single sample from *Klattia partita* consisted of only 5.5 μl of nectar of 15% sugar concentration. Excluding *Klattia* species, the size of a flower correlates positively with nectar volume, thus the larger the flower the greater the quantity of nectar produced.

Volume and sugar concentration of nectar vary among bird flowers, even within the same genus (Table 4), sometimes quite extensively, a feature

also noted by JOHNSON & BOND (1994). Among the 15 *Gladiolus* species examined, plants secrete between 3 µl to 36 µl of fluid, ranging in concentration from 18% to up to 35% dissolved sugar.

Sugar analyses vary both between and within genera. Nectar of *Chasmanthe* species are hexose-dominant, and *Babiana* and *Tritoniopsis* have sucrose-rich to sucrose-dominant nectar. In contrast, the genera *Klattia* and *Witsenia* have hexose dominant nectar. Within *Watsonia* and *Gladiolus* selected species may have either sucrose-dominant or hexose-dominant nectars. Sucrose production is most variable within *Gladiolus* and correlates with sectional affinity. Three bird pollinated species of section *Hebea* are the only species in the genus that have hexose-rich or hexose-dominant nectar (*G. cunonius, G. saccatus, G. splendens*).

DISCUSSION

Pollination by sunbirds appears to be a recurrent strategy in the Iridaceae of temperate southern Africa. We suspect that red-flowered or red-bracted *Gladiolus* species in tropical Africa (GOLDBLATT 1996) are also bird-pollinated and these species grow well within the geographic range of the African Nectarinidae. In contrast, bird pollination is rare in the family outside Africa. Outside Africa, ornithophily is evidently restricted to the four species of *Tigridia* in Mexico and Guatemala that were once assigned to a separate genus, *Rigidella*. The presumption of hummingbird pollination is based on the combination of red flowers, abundant nectar in a narrow floral cup, and well exserted, sturdy stamens and styles (CRUDEN 1971), but there appear to be no foraging observations to support the hypothesis of hummingbird pollination.

The concentration of bird-pollinated Iridaceae in subfamily Ixioideae may represent, in part, a simple genetic constraint. A perianth tube and floral nectar is present in all members of subfamily Ixioideae, preadapting taxa to one aspect of pollination by long-tongued nectarivorous birds. In contrast, a perianth tube is absent in nearly all African Iridoideae and nectar production is limited in quantity. We presume that the evolution of

bird pollination from ancestors with perianth tubes and floral nectar requires fewer steps than the evolution of bird pollination from ancestors with free tepals. This probably explains why bird pollination has also evolved in members of subfamily Nivenioideae which likewise have flowers with perianth tubes and produce ample nectar.

Bird pollination mechanisms in the Ixioideae, and to a lesser extent the Nivenioideae, follows most of the standard suite of characters associated (RAVEN 1972) with two important exceptions. First, red to orange pigmentation is not characteristic of *Witsenia*, two *Klattia* species, and some *Watsonia* species. Is this because these species bloom when competitive, nectar-robbing insects are absent and/or reduced in number. Recent evidence (CHITTKA & WASER 1997) suggests that large bees can see into the red end of the spectrum but tend to avoid flowers of this color. Unfortunately this does not provide an explanation for the absence of insects on blue, yellow, pink or mauve irids that are bird pollinated.

Klattia and many bird pollinated *Watsonia* species flower in summer when native *Apis* and *Amegilla* species are active. Floral form is probably sufficient to discourage insect nectar robbers on *Witsenia* due to the tightly closed tepals and the large leathery bracts. While the brush inflorescences of *Klattia* readily offer anthers to pollen robbery by bees the thick, tightly sheathing spathes presumably preclude nectar theft by long-tongued insects.

Of greater importance, the nectar chemistry of bird-pollinated Iridaceae fails to follow predictions for nectar consumed by passerines. Hexose-rich and hexose dominant nectars are predicted in flowers pollinated by perching birds (BAKER & BAKER 1983, 1990). Instead, as shown by JOHNSON & BOND (1994) hexose and sucrose ratios vary broadly between and within some genera. This is particularly surprising when we remember that all avian pollinators of the southern African Iridaceae belong to the same genus. The higher levels of sucrose in *Tritoniopsis* and *Watsonia* might be explained by the fact that both sunbirds and the butterfly, *Aeropetes,* may be co-pollinators of some species (JOHNSON & BOND 1994). However, this cannot be used to explain the extraordinarily high sucrose ratios in

taxa that are pollinated exclusively by sunbirds. This includes *Babiana ringens* and five *Gladiolus* species, including *G. watsonius* which has only almost no measurable quantities of hexose sugars based on our limited sampling. Particularly high concentrations of dissolved sugars are characteristic of the *Gladiolus* species that flower relatively early in the season in the winter-rainfall zone, July to September. This is months before *Aeropetes* is on the wing and there is no question of this species sharing the pollination of spring-flowering *Gladiolus*. Differences in nectar chemistry of flowers using the same pollinators is often explained in terms of their phylogenetic history. However, this argument cannot be made for those *Gladiolus* species of section *Hebea* that have hexose dominant nectar, exceptional in the genus. This shift in nectar chemistry may be the result of pollinator driven selection.

JOHNSON & BOND (1994) discuss the pollination of red flowers by the satyrid butterfly, *Aeropetes*, in southern Africa and their observations and interpretations strongly indicate that this large, energetic insect has been an important selective force for pollination adaptations in several angiosperm lineages. They conclude, however, that most of the several red-flowered species of *Tritoniopsis* are primarily pollinated by sunbirds. We suggest, instead, that of those that flower in the late summer, at least *T. burchellii* and *T. triticea* may be predominantly pollinated by *Aeropetes* or combine the pollination of flowers by both sunbirds and this large butterfly. These two species have smaller flowers than those usually associated with bird pollination. Moreover, when faced with a choice of large, scarlet flowered *Watsonia schlechteri* and deep red-flowered *T. triticea* at Hermanus, we found that *Aeropetes* consistently visited the *Tritoniopsis* and *Nectarinia violacea* the *Watsonia*. *Aeropetes* shows such a strong attraction to red flowers that it is no surprise that it has been observed and captured on several species of *Iridaceae*, the flowers of which seem adapted to bird pollination by virtue of their large size and huge quantities of nectar. *Aeropetes* has been noted occasionally visiting *Watsonia tabularis* (STEINER, pers. comm. and unpubl. obs.) and some other red- or orange-flowered *Watsonia* species that bloom when

Aeropetes is on the wing in late summer and autumn. *Aeropetes* has also been seen settling on *Gladiolus flanaganii* in eastern southern Africa (VLOK in JOHNSON & BOND 1994), a putatively bird-pollinated species that has a long floral tube and thickened perianth (GOLDBLATT & MANNING 1998).

The classic literature on pollination biology indicates that bird-pollinated-flowers and butterfly-pollinated flowers often share characters (FAEGRI & VAN DER PIJL 1979). Nectar-feeding birds and the majority of butterflies are diurnal foragers and flowers pollinated by these animals have tubular and/or funnel-shaped, red perianths. Hummingbirds and butterflies are known to share nectar sources within the Polemoniaceae in North America (GRANT & GRANT 1965). In fact, insects and birds are commonly incorporated within the spectra of pollen vectors of the same dicot taxa. For example, pollination systems that combine hummingbirds and bees have been well documented in the genera *Fuchsia* (Onagraceae) and *Impatiens* (Balsaminaceae) (BREEDLOVE 1969; SCHEMSKE 1978). Final clarification of the respective roles of *Aeropetes* butterflies versus sunbirds in the pollination of species of Iridaceae must be determined by a combination of consistent, season long observations and pollen load analyses.

The discrepancy between the number of African genera in which bird pollination occurs estimated by VOGEL (1954) and the figures given here is largely due to changes in taxonomy of the family, although VOGEL did not realize that the flowers of *Klattia* are adapted for bird pollination. Re-examination of several genera of the family that were evidently founded solely on characters that are adaptations for bird (and sometimes butterfly) pollination resulted in a reappraisal of the generic systematics of the Iridaceae. GOLDBLATT & DE VOS (1989) and GOLDBLATT (1990b) argued that adaptations for bird pollination alone were not sufficient grounds for the recognition of a genus. They argued that the genera *Anapalina*, *Antholyza*, *Anaclanthe*, *Anomalesia*, *Homoglossum* (including *Petamenes*), and *Oenostachys*, were such genera and that they were nested within larger genera of which they were highly specialized species,

adapted for bird pollination. These six genera are now submerged within *Babiana*, *Gladiolus*, or *Tritoniopsis*, all of which consist of species with a variety of different pollination systems and in which long-tongued bee pollination appears to be ancestral (GOLDBLATT et al. 1998b and unpublished).

More important, even within genera confidently assumed to be monophyletic, adaptations to bird pollination are diverse and are not necessarily restricted to one lineage. In *Watsonia*, which comprises 52 species, ornithophily may have evolved four times and 24 species are inferred to be pollinated by birds (GOLDBLATT 1989). In *Gladiolus*, a genus dominated by bee pollination (GOLDBLATT et al. 1998b), 20 species are inferred to be pollinated by birds. GOLDBLATT & MANNING (1998) suggest that the strategy evolved independently in four sections of *Gladiolus*, and in one of these, section *Homoglossum*, in two separate series. Only the smallest genera, *Chasmanthe* and *Klattia*, each with three species, and the monotypic *Witsenia*, appear to be uniformly bird-pollinated. In *Crocosmia* and *Tritoniopsis* we have no reason to suspect more than a single origin of bird pollination in each genus although this possibility cannot be excluded. Thus flowers adapted for bird pollination would appear to have evolved independently at least 13 times in subfamily Ixioideae. In subfamily Nivenioideae bird flowers may have evolved just twice, in *Klattia* and in *Witsenia*, or only once in the common ancestor of these two genera.

Although the adaptations for bird pollination are striking, and conspicuous in the African Iridaceae, this pollination system assumes relatively low importance in the family. Just 64 species out of the over 1000 species in southern Africa, 6.4% of the total, are now believed to be pollinat-ed by sunbirds. In the Iridaceae other specialist pollination systems assume greater importance. At least 95 species of southern African Iridaceae have flowers adapted exclusively for long-tongued fly pollination (GOLDBLATT & MANNING, ms.) and studies currently in progress (GOLDBLATT et al. 1998a) indicate that an even greater number of species in the family have flowers adapted for pollination by hopliine beetles alone or the unusual combination of hopliine beetles and short-proboscid tabanid flies. Even more important in the family is the anthophorine bee pollination system, which we argued elswhere (GOLDBLATT et al. 1998b) was also a specialist pollination system. Despite the striking adaptations associated with bird pollination in the Iridaceae, the strategy is relatively poorly represented in the family and assumes importance only in *Tritoniopsis* and *Watsonia*, excepting of course for *Chasmanthe*, *Klattia* and *Witsenia* in which it is the sole pollination system and a defining feature of these taxa.

Acknowledgments

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