Aliso: A Journal of Systematic and Evolutionary Botany

Volume 22 | Issue 1 Article 35

2006

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Aliso 22, pp. 434–444

THE ROLE OF PHYLOGENETIC CONSTRAINTS IN THE EVOLUTION OF POLLINATION MECHANISMS IN IRIDACEAE OF SUB-SAHARAN AFRICA

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ABSTRACT

Novel, specialized systems exploiting bibionid flies, oil-collecting bees, wasps, or crepuscular settling moths as pollen vectors are added to the range of recorded pollination mechanisms in sub-Saharan Africa Iridaceae, while knowledge of the pollination of previously understudied genera such as *Aristea, Babiana, Ferraria, Hesperantha,* and *Tritoniopsis* is expanded. The pollination of 357 species of the sub-Saharan African Iridaceae now includes 17 discrete systems. Based on repetitive interlinked suites of floral attractants and rewards we now infer pollination mechanisms for an additional 883 species. Many pollination systems recur in genera containing >10 species. The ancestral pollination in African Iridaceae, and also the most common one, involves large, long-tongued bees that contact anthers or stigmas passively while foraging for nectar. Some 182 species (in 11 genera) lack nectar or oil and pollinators forage preferentially for pollen. Our earlier hypothesis that the diversity of pollination mechanisms within a lineage increases via adaptive radiation and/or character displacement involving simple shifts in floral presentation is expanded to include the role of phylogenetic constraint. Specifically, possession of the meranthium flower in *Moraea* (ca. 195 spp.) and *Ferraria* (ca. 14 spp.) of subfamily Iridoideae limits the number of pollination shifts in these genera. More pollination shifts occur in subfamily Crocoideae (ca. 1000 spp.) because the ancestral flower includes tepals united basally into a floral tube and bilateral symmetry. With 16 derived pollination mechanisms described for this family in sub-Saharan Africa it is obvious that phylogenetic constraint is sufficiently flexible to explain the shifts in pollination mode.

Key words: Coleoptera, Diptera, evolution, Hymenoptera, Iridaceae, Lepidoptera, phylogeny, pollination mechanism.

INTRODUCTION

Iridaceae (est. 65 genera, 1890 species) include some 37 genera and 1190 species in sub-Saharan Africa. The family reaches its greatest diversity in southern Africa, where it displays its greatest variation in vegetative and floral characters. In a previous review of pollination in the family we related these floral characters to suites of morphological and biochemical modes of floral presentation representing five broadly defined pollination syndromes occurring in 21 genera of temperate, winter dry, or Mediterranean habitats (Bernhardt and Goldblatt 2000).

These five syndromes (sensu Faegri and van der Pijl 1971) are no longer adequate to define floral evolution in African Iridaceae. Continued fieldwork on the native genera indicates that some modes of floral presentation reflect both parallel and convergent evolution in which only a few species or closely related insects or birds remain the primary pollinators of an expanding diversity of co-blooming plant species. In addition, three of the five broad syndromes that we discussed (Bernhardt and Goldblatt 2000) require clarification and subdivision. Wasp pollination must also be added to the list of novel syndromes.

More important, as fieldwork on selected genera continues it has become possible to infer pollination syndromes of species not yet studied based on shared suites of stereotyped characters. This makes it easier to determine the comparative roles of active vs. passive anther contact (sensu Bernhardt 1996) as pollination syndromes shift (sensu Stebbins 1970) within the same lineage.

It is now evident that some relatively large genera (e.g., *Lapeirousia, Moraea, Romulea, Watsonia,* etc.) fail to exploit one or more of the most dependable and/or common floral foragers such as long-proboscid flies, birds, or scarab beetles as pollen vectors (Table 1). Consequently, the original hypothesis (Bernhardt and Goldblatt 2000) that pollinator shifts occur predictably with speciation patterns based primarily on adaptive radiation and/or character displacement may require some modification. The unexpected absence of "predictable" pollination shifts in the most speciose genera become clearer if they are viewed within the context of their inherited floral architecture (bauplan) based on phylogenetic constraint.

Finally, there is a much broader advantage to reviewing and expanding pollination systems within African Iridaceae as interpreted through the lens of phylogenetic constraint. It allows us to readdress directly the ongoing debate as to whether floral evolution within most angiosperm lines reflect a trend towards generalist (sensu Waser et al. 1996) or specialist (sensu Johnson and Steiner 2000) pollination systems (see also Bernhardt and Goldblatt 2000).

MATERIALS AND METHODS

Field and Laboratory Assessment of Pollination Ecology

The floral biology of 357 species of the sub-Saharan African Iridaceae was examined in situ and in appropriate laboratories in South Africa and North America over a period of 16 years. Techniques for observing pollinators, capturing

Table 1. Comparative pollination systems of selected genera of sub-Saharan African Iridaceae. The long-proboscid fly pollination systems follow the definitions established by Goldblatt and Manning (2000). Note: the passive pollination system that involves large-bodied, long-tongued Apid bees occasionally also includes tabanid and nemestrinid flies with short probosces. There is no evidence that these flies are a normal part of this system but, nevertheless, they function exactly like Apid bees and probably successfully accomplish pollen transfer. We consider them part of the Apid bee pollination system. An exception is *Nivenia binata* Klatt, which is pollinated consistently by both long-proboscid flies and large anthophorine bees. Genera not included: *Bobartia* L. (15 spp.); *Cyanixia* Goldblatt & J. C. Manning (1); *Devia* Goldblatt & J. C. Manning (1); *Dierama* K. Koch (44); *Dietes* Salisb. ex Klatt (6); *Syringodea* J. D. Hook. (8); *Zygotritonia* Mildbr. (4). Apid. = *Apis* and other large-bodied, long-tongued Apidae; Apid.Buzz = Anthophorine bees using vibratile pollination; Bibionid. = march flies (Bibionidae); Bird = sunbirds (Nectarinidae); Gen. = generalist (pollinators from more than two pollinator classes); Lepid.B = diurnal Lepidoptera, i.e., butterflies; Lepid.M, = crepuscular and nocturnal Lepidoptera, i.e., moths; Oil.CB-Apid. = oil-collecting *Rediviva* (Melittidae) and Apid bees; LPF_1 = the *Prosoeca peringueyi* pollination system; LPF_2 = the *Prosoeca ganglbaueri* pollination system; LPF_3 = the *Moegistorhynchus–Philoliche* pollination system; SPDip. = short-proboscid flies (Calliphoridae, Muscidae, Scathophagidae); Scarab. = hopliine scarab beetles (Scarabaeideae–Hopliini); Fem.Apoid. = female bees including short-tongued female bees of various families and long-tongued Apidae of both sexes or workers; wasp = Eumenidae and Masaridae.

Genus	No. of species studied	No. studied plus inferred/total	Pollinators (in order of importance)
Aristea Aiton	12	50/50	Fem.Apoid. (41), Apid.Buzz (4), Scarab. (4), LPF_3 (1)
Babiana Ker Gawl.	40	79/79	Apid. (44), Fem.Apoid. (5), Scarab. (8), LPF_1 (12), Lepid.M (4), LPF_3 (3), Bird (3)
Chasmanthe N. E. Br.	2	3/3	Bird (3)
Crocosmia Planch.	5	7/8	Bird (3), Apid. (2), Lepid.B (2)
Duthiastrum M. P. de Vos	1	1/1	Fem.Apoid (1)
Ferraria Burm. ex Mill.	8	10/12	SPDip. (7), wasp (2), Apid. (1)
Freesia Klatt	3	12/15	Apid. (12), Lepid.B (2), Lepid.M (1)
Geissorhiza Ker Gawl.	14	17/85	Apid. (6), Scarab. (4), LPF_3 (6), LPF_1 (1)
Gladiolus L.	78	161/165	Apid. (87), Bird (20), LPF_2 (15), LPF_3 (14), (only southern Africa) Lepid.M (11), Lepid.B (9), Fem.Apoid. (4), Apoid./Scarab (1)
Hesperantha Ker Gawl.	25	79/79	Apid. (33), Lepid.M (24), LPF_2 (9), LPF_1 (3), LPF_3 (3), Apoid./Scarab. (3), Scarab. (2), Lepid.B (1)
Ixia L.	21	50/50	Scarab. (20), Apid. (11), Apid.Buzz (9), LPF_3 (5), Apoid./Scarab. (4), Lepid.B (1)
Klattia Baker	2	3/3	Bird (3)
Lapeirousia Pourr.	20	41/41	Gen. (15), LPF_1 (8), Apid. (7), Lepid.M (5), LPF_3 (4), Scarab. (2)
Melasphaerula Ker Gawl.	1	1/1	Bibionid. (1)
Micranthus Eckl.	2	3/3	Gen. (3)
Moraea Mill.	36	195/195	Apid. (108), Fem.Apoid. (41), Apoid./Scarab. (30), Scarab. (14), SPDip. (2)
Nivenia Vent.	5	10/10	Apid. (5), LPF_2 (4), Apid./LPF (1)
Pillansia L. Bolus	1	1/1	Gen. (1)
Radinosiphon N. E. Br.	1	1/2	LPF_2 (1)
Romulea Maratti	31	75/75	Fem.Apoid. (47), Apoid./Scarab. (15), Scarab. (8), LPF_1 (3), LPF_3 (1)
Savannosiphon Goldblatt & W. Marais	0	1/1	Lepid.M (1)
Sparaxis Ker Gawl.	13	15/15	Apid. (5), Apoid./Scarab. (4), Scarab. (3), LPF_1 (3)
Thereianthus G. J. Lewis	1	1/7	Scarab. (1)
Tritonia Ker Gawl.	7	14/28	Apid. (5), LPF_3 (4), Scarab. (3), Fem.Apoid. (1), LPF_1 (1)
Tritoniopsis L. Bolus	14	24/24	Apid. (12), Lepid.B (4), Bird (3), LPF_3 (3), Lepid.M (1), Oil.CB-Apid. (1)
Watsonia Mill.	12	51/51	Bird (26), Apid. (18), LPF_2 (3), LPF_3 (3), Lepid.B (1)
Witsenia Thunb.	1	1/1	Bird (1)
Xenoscapa (Goldblatt) Goldblatt & J. C. Manning	1	2/2	LPF_1 (1), Lepid.M (1)
	357	883/1007	

pollinators, removing and identifying pollen grains carried by floral foragers, collecting and analyzing nectar, detecting floral fragrance, recording pigmentation patterns, tagging individual flowers to record floral lifespan and/or results of natural vs. manipulative pollen-stigma interactions and fruit set follow Goldblatt and Bernhardt (1990) and Goldblatt et al. (1995, 1998*a*, *b*).

Inference of Pollination Mechanisms

The floral biology of an additional 883 species within the Iridaceae of sub-Saharan Africa was inferred by sorting the character suites expressed by the 357 species already studied into floral characters into recognizable and repetitive syndromes. The character suites expressed by each syndrome

Table 2. Distribution of active vs. passive modes of pollen dispersal and nectar analyses in selected species of sub-Saharan African Iridaceae. Nectar is produced from perigonal nectaries in Irideae but from septal nectaries in Nivenioideae and Crocoideae. Note that except in tribe Irideae, production of hexose sugars is associated with pollination by birds or large butterflies. Some species using these two pollination systems, however, often produce sucrose-rich or -dominant nectar (Goldblatt et al. 2001). Active pollination systems include exclusively female bee system plus the combined bee/hopliine beetle system. Generalist systems may have an active component, but we prefer to treat this as a passive system. *Proportions of sugars dissolved in water (sucrose/glucose + fructose; see Baker and Baker 1983, 1990); HD = hexose sugars dominant (>0.1); HR = hexose-rich (0.1–0.49); SR = sucrose-rich (0.5–0.99); SD = sucrose-dominant (>0.99); NA = nectar lacking or trace too small to sample.

Genus	Active (pollen collecting) (observed plus inferred)	Passive (nectar foraging)	No. of species with nectar sugar groups*				
			HD	HR	SR	SD	None (or trace)
Irideae							
Ferraria	0	10	4	0	0	0	0
Moraea	41	154	6	0	0	0	5
Nivenioideae							
Aristea	45	5	0	0	1	0	49
Klattia	0	3	3	0	0	0	0
Nivenia	0	10	0	0	0	4	0
Witsenia	0	1	1	0	0	0	0
Crocoideae							
Babiana	5	74	0	0	0	17	4
Chasmanthe	0	3	2	1	0	0	0
Crocosmia	0	8	0	0	1	0	0
Duthiastrum	1	0	0	0	0	0	0
Geissorhiza	3	9	0	0	0	6	trace (3)
Gladiolus	4	161	2	2	4	61	trace (3)
Hesperantha	3	76	0	2	1	3	0
Ixia	13	37	0	0	1	3	9
Lapeirousia	0	41	0	2	2	10	0
Melasphaerula	0	1	0	0	0	0	trace (1)
Pillansia	0	1	0	0	0	0	trace (1)
Romulea	62	10	0	0	0	2	8
Sparaxis	4	11	0	0	0	3	0
Thereianthus	0	2	0	0	0	2	trace (1)
Tritonia	1	27	0	0	0	4	0
Tritoniopsis	0	24	0	0	0	7	0
Watsonia	1	50	0	0	1	5	0
Total:	183	684	14	7	11	127	71

were then used as a template for the remaining 883 species. Each character suite included floral symmetry (radial vs. bilateral), the position of the flower relative to its peduncle (erect, horizontal, nodding), relative lengths of the floral tube, presence of stigmatic crests, floral phenology (time of day in which tepals expanded) and life span, pigmentation pattern, presence of floral nectar and/or oil, mode of anther dehiscence, and the symmetry and relative positions of dehiscent stamens to the receptive stigma.

RESULTS

Novel Modes of Pollination in Iridaceae of Sub-Saharan Africa and Pollinator Shifts in Understudied Genera

Bee pollination.—In our previous review (Bernhardt and Goldblatt 2000) we noted that 14 genera of African Iridaceae contain one or more species pollinated primarily by bees. Sixteen genera with at least one bee-pollinated species are now known to have bee-pollinated species (Table 1). Bees that pollinate the sub-Saharan African Iridaceae represent six native families including: Apidae s.l. with their large bodies and long tongues; Andrenidae, Mellitidae, and Megachilidae, which include bees with large bodies and short tongues; and Colletidae and Halictidae, with bodies less than 7 mm in length with short mouthparts. Bees forage on nectarless flowers in Iridaceae for pollen exclusively (resulting in active anther contact sensu Bernhardt 1996) or predominantly for nectar (passive anther contact) in nectar-rich species. These two modes of anther contact intergrade when some bees forage mainly for pollen in species in which the stamens form a prominent column but trace amounts of nectar are also offered, e.g., *Moraea bifida* (L. Bolus) Goldblatt, *M. minata* Sweet (Goldblatt and Bernhardt 1999), many *Romulea* species. Species with staminal columns or prominently displayed anthers in radially symmetric perianths, with or without small quantities of nectar, are pollinated by female bees collecting pollen for their offspring based on active anther contact (Table 2, 3). Nectar foraging is a coincidental activity, not essential for pollen transfer. Bee pollination, in general, remains the most common mode of pollination in Iridaceae of sub-Saharan Africa with >54% of species under consideration pollinated exclusively by at least

Table 3. Frequency of different pollination systems in selected genera of sub-Saharan African Iridaceae arranged in descending order of importance. Note that when combined, the three long-proboscid fly systems, with 111 species, are third in order of importance. Our sample includes 918 species, or 79% of the estimated 1165 species of Iridaceae in sub-Saharan Africa.

Pollination system	No. of plant species using each system
Apid. (*Apis* and other large-bodied, long-tongued Apidae)	366
Fem.Apoid. (short- and long-tongued female bees of various families)	140
Scarab. (Scarabaeideae: Hopliini—monkey beetles)	69
Bird (Nectarinidae—sunbirds)	62
Apoid./Scarab. (bees and monkey beetles)	57
Lepid.M (crepuscular and nocturnal Lepidoptera—moths)	48
LPF_3 (*Moegistorhynchus* spp., *Philoliche gulosa,* and *P. rostrata*)	47
LPF_1 (*Prosoeca peringueyi* and *P.* sp.)	32
LPF_2 (*Prosoeca ganglbaueri, P. robusta, Stenobasipteron,* etc.)	32
Lepid.B (large diurnal Lepidoptera—butterflies)	20
Gen. (generalist, pollinators from more than two pollinator classes)	19
Apid.Buzz (Anthophorine bees using vibratile pollination)	13
SPDip. (short-proboscid Calliphoridae, Muscidae, Scathophagidae)	9
Eumenid. (wasps of the families Eumenidae and Masarinae)	2
Bibionid. (Bibionidae—march flies)	1
Oil.CB-Apid. (oil-collecting *Rediviva* (Melittidae) and Apid bees)	1
Apid.-LPF (combined large-bodied Apid bee and long-proboscid fly)	1
	919

one bee species and 62% pollinated by a combination of bees and other animals (Table 3).

A few *Moraea* species have been recorded visited by oil-collecting bees (Melittidae) in the genus *Rediviva* although *Moraea* species do not secrete nonvolatile oils (Bernhardt and Goldblatt 2000). These bees also gather pollen, and consume nectar as part of their foraging patterns. While nonvolatile oils are secreted by trichomes on the staminal filaments or tepal claws of many genera of South American Iridaceae, including several species of *Sisyrinchium* L., *Tigridia* Juss., and their allies (all subfamily Iridoideae; see Vogel 1974), such oil secretion is limited to just one species in the Old World.

The first and only record of nonvolatile oil secretion as a reward in African Iridaceae was described in *Tritoniopsis parviflora* (Jacq.) G. J. Lewis by Manning and Goldblatt (2002). This species, endemic to the Cape region of South Africa, has a bilaterally symmetrical (gullet-flag type) perianth and the oil is secreted by epithelial eliaphores distributed over proximal portions of the tepals and the throat of the perianth tube. Small quantities of true nectar (30–35% dissolved sugars) are also produced by septal nectaries and retained in the floral tube. The only insects found to carry the pollen of this species on the dorsal side of the thorax (where the anthers would brush against a forager) were female *Rediviva gigas* Whitehead and Steiner, a large-bodied, oil-collecting bee. However, pollination by nectar foraging bees is inferred because *T. parviflora* grows in areas where *R. gigas* is absent, and plants still set fruit.

Bee-pollinated *Sparaxis galatea* Ker Gawl. was thought to have nectarless flowers and was interpreted as a potential Batesian mimic of co-blooming, nectariferous *Gladiolus* species (Goldblatt et al. 2000*b*) "tricking" bees into visiting a flower with an empty nectar tube. It has since been found that this species secretes significant amounts of nectar, and thus fits within the normal pattern for pollination by large-bodied, long-tongued bees.

Butterfly and moth pollination.—Reviewing pollination by Lepidoptera in Iridaceae of southern Africa, Bernhardt and Goldblatt (2000) subdivided the syndrome into two main systems. One group of species blooms during the day, are often brightly pigmented, usually lack a discernible scent, have floral tubes of varying lengths, and are pollinated by true butterflies or less often by a combination of butterflies, long-tongued bees, diurnal, and even short-tongue moths. Scarlet, narrowly funnel-shaped and scentless flowers in the southern African winter-rainfall zone–typically with bright red flowers with white splashes on the tepals—are pollinated primarily by the satyrid butterfly, *Aeropetes* (*Meneris*) *tulbaghia* L. (Table 1; Goldblatt and Manning 2002, unpubl. data). In eastern southern Africa similarly pigmented flowers, as well as orange flowers, may also be pollinated by *Papilio* L. species (Papilionidae), evidently uncommon in the winter-rainfall zone. Examples of large-flowered Iridaceae of eastern southern Africa pollinated by *Papilio* spp. include *Crocosmia aurea* (Pappe ex J. D. Hook.) Planch. (Goldblatt et al. 2004*a*) and *Hesperantha coccinea* (Backh. & Harv.) Goldblatt & J. C. Manning (Goldblatt et al. 2004*b*).

The second group shows crepuscular or nocturnal anthesis combined with a pale-colored or whitish perianth (sometimes with dark mottling), a relatively long floral tube, and usually strong scents. Most are pollinated by night-flying moths with probosces from 2.8–10 cm in length. The majority of insect visitors to these flowers are hawk moths (Sphingidae), which hover while foraging for nectar (Table 1).

A third mode of moth pollination has subsequently been recognized for some species in the genera *Babiana* and *Hesperantha* (Goldblatt et al. 2004*b*, unpubl. data). In *Hesperantha,* relatively small flowers open in the late afternoon or soon after sunset, have a whitish or pale yellow perianth, are strongly scented, and have relatively short perianth tubes (mostly 5–12 mm long) that are typically shorter than their tepals. While bees sometimes forage for pollen and nectar on these flowers while daylight persists they are replaced after sunset by small, settling (non-hovering) moths in the families Adelidae, Drepanogynidae, Geometridae, Noctuidae, and Pyralidae. These moths have probosces only 4–12 mm in length. As moths forage for nectar exclusively, anther contact remains passive (Table 2) unless bees arrive before dusk. When systems pollinated by these settling moths are combined with earlier studies on pollination by hawk moths

we estimate that less than 6% of the species of Iridaceae in our sample have crepuscular-nocturnal moths as primary pollinators (Table 3).

Fly pollination.—Pollen dispersal by dipterans was variable and distinctive in the Africa Iridaceae and we initially distinguished two modes of floral presentation in flowers pollinated by Diptera (Bernhardt and Goldblatt 2000). Sapromyiophily (sensu Faegri and van der Pijl 1971) was described for *Ferraria crispa* Burm. Here radially symmetric flowers with a wide, shallow floral cup, putrescent odor, and lurid coloration are pollinated by large-bodied dung, carrion, and flesh flies (Calliphoridae, Muscidae, and Scathophagidae) that land on the tepals to forage for nectar.

A second, equally specialized dipteran system exploits flies with probosces mostly 2–4 times the length of the insect's body and the dominant pollinators belong to the genera *Philoliche* Wiedemann (Tabanidae), *Prosoeca* Schiner, and *Moegistorhynchus* Wiedemann (Nemestrinidae). These flies usually settle on the tepals to feed, although they are also reported to show some capacity for hovering while foraging (Struck 1997). As these insects consume nectar exclusively, anther contact remains passive (Table 1, 2) although most dramatic. Floral scent is weak and difficult to discern, or evidently lacking. Floral tubes are exaggerated in length while tepals may show either radial or bilateral symmetry. Floral pigmentation patterns differ within this system and appear to reflect the preferences of dominant foragers. Thus, the color patterns expressed by flowers pollinated primarily by *Prosoeca peringueyi* Lichtwardt differ significantly from those species pollinated by *Philoliche* and *Moegistorhynchus*. Color patterns differ less obviously between species pollinated by *Prosoeca* species belonging to the *P. ganglbaueri* Lichtwardt pollination group (Goldblatt and Manning 2000).

We estimate that some 13% of the species of African Iridaceae in the genera under consideration have flies as primary or secondary pollinators. This means that flower-visiting flies are the third most common group of pollinators after bees and hairy scarab beetles, but species pollinated primarily, or in part, by long-proboscid flies (ca. 12%) far outnumber sapropmyiophilous systems (ca. 1%: Table 3).

Of greater importance, since our initial review (Bernhardt and Goldblatt 2000) additional species of long-proboscid flies in the Nemestrinidae, including the genus *Stenobasipteron* Lichtwardt, have been found to be the pollinators of species with exaggerated floral tubes. Long-proboscid fly pollination has now been subdivided into three separate, non-overlapping systems based in floral pigmentation patterns, seasonal and geographical distribution, and species of fly pollinators. In the *Prosoeca peringueyi* pollination system, *P. peringueyi,* and *P.* sp. nov. pollinate a range of species with deeply pigmented, dark blue to violet or purple flowers with contrasting pale nectar guides. Conversely, within the *Philoliche–Moegistorhynchus* pollination system, *Philoliche gulosa* Wiedemann, *P. rostrata* L., *Moegistorhynchus longirostris* Wiedemann, and other *Moegistorhynchus* spp. visit and pollinate white to pale pink flowers with reddish markings. Finally, within the *Prosoeca ganglbaueri* pollination system, flies—including *Prosoeca ganglbaueri, P. longipennis* Loew, *P. robusta* Bezzi, and *Stenobasipteron wiedemannii* Lichtwardt—pollinate pale to deep pink or rarely blue flowers that often have pink to red or nectar guides.

Pollination-by-deceit may also occur in the nectarless flowers of *Hesperantha pubinervia* L. Bolus and *H. scopulosa* Hilliard & B. L. Burtt. Their modes of floral presentation resemble those of other co-blooming, nectar-secreting plants including other *Hesperantha* species, belonging to local guilds dependent on the long-proboscid fly, *Prosoeca ganglbaueri,* for pollination (Goldblatt et al. 2004*b*). Pollination-by-deceit occurs in terrestrial orchids of southern Africa (e.g., *Disa* P. J. Bergius spp.) pollinated by long-proboscid flies: this is the first documentation of the syndrome in Iridaceae.

A new mode of fly pollination has been described for the monotypic genus *Melasphaerula* (Goldblatt et al. 2005*a*). *Melasphaerula ramosa* (Burm. f.) Ker Gawl. appears to be pollinated exclusively by the small-bodied (4.5–5.0 mm long), short-proboscid March fly, *Bibio longirostris* Macquart (Bibionidae). The anthers swab the back of the flies while they forage for nectar but the short-tube, gullet flowers are unusually small (8–10 mm long) and produce only trace amounts of nectar. The bilateral symmetry of both the perianth and androecium is atypical for pollination by short-proboscid flies. Floral presentation in *Melasphaerula* recalls that of the southern African orchid, *Disa obtusa* Lindl., also pollinated by a bibionid fly, in this case *Bibio turneri* Edwards (Johnson and Steiner 1994).

Wasp pollination.—Until recently no examples of wasp pollination had been recorded in African Iridaceae. However, pollination by masarine wasps (Masaridae) occurs commonly in representatives of unrelated families native to the southern African flora (see Gess and Gess 1989). Furthermore, the wide, bowl-shaped flowers of *Ferraria variabilis* Goldblatt & J. C. Manning (as *F. divaricata* Sweet) were reported to be visited by females of the masarine species, *Jugurtia koeroegabensis* Gess, by Gess (1997). Male and female *Delta* Saussure spp. and *Allepipona erythrospila* Cameron (Eumenidae) have also been captured recently while visiting *F. variabilis,* while *Delta caffer* L. has been captured visiting *F. divaricata* (Goldblatt and Manning unpubl. data). While broadly resembling the fly-pollinated *Ferraria* species in their dull coloration, the flowers of *F. divaricata* and *F. variabilis* lack a putrid odor and produce ample quantities of extremely dilute nectar (typically 4–9% sucrose equivalents). This fluid accumulates in a pool at the base of the wide, but relatively deep floral cup. In contrast, while fly pollinated *Ferraria* species usually have putrid smelling flowers they always have a much shallower floral cup in which more concentrated droplets of nectar (>50% sucrose equivalents) are produced over the surfaces of large, perigonal nectaries that cover about half the area of the claws. We speculate that the water in the unusually dilute nectar produced by *F. divaricata* and *F. variabilis* is the real reward for *Delta, Jugurtia* Saussure, and *Allepipona* Giordani Soika species. *Delta* and *Allepipona* are potter wasps and require a water source for both personal consumption in a dry habitat and for processing soil to build mud nests. In particularly dry areas, such as those found within the interior west coast of southern Africa, which is the semi-arid habitat favored by

Ferraria, there is a low frequency of water sources and even those present may not be available to potter wasps due to the considerable distances involved.

Self-compatibility and facultative autogamy.—Although limited information is available on pollen-pistil interactions in African Iridaceae, Goldblatt et al. (1995, 2000*b*) report that some species pollinated by long-proboscid flies and long-tongued bees are facultatively autogamous. These species, which typically have smaller, less conspicuous flowers than their immediate relatives, include *Lapeirousia jacquinii* N. E. Br., *L. oreogena* Schltr. ex Goldblatt, *Sparaxis meteler-kampiae* (L. Bolus) Goldblatt & J. C. Manning (all pollinated by *Prosoeca peringueyi*), *S. parviflora* (G. J. Lewis) Goldblatt, and *S. villosa* (Burm. f.) Goldblatt (pollinated by *Apis* workers or anthophorines, respectively). These species belong to genera in which other species have been confirmed to be self-incompatible. Therefore, mechanical self-pollination most probably represents a fail-safe mechanism in the absence of adequate pollinator activity. Similarly in *Moraea,* a genus in which self-incompatibility is the rule (Goldblatt 1981, 1987), several species have been found to be self-compatible and their flowers set seed even when their insects are excluded. Most of these species also have small, less brightly colored flowers than their closest relatives. Of these, *M. albiflora* (G. J. Lewis) Goldblatt, *M. demissa* Goldblatt, and *M. minor* (Eckl.) Goldblatt receive some visits from pollinating insects (Goldblatt et al. 2005*b*), and are best regarded as facultatively autogamous. There may be a correlation between karyology and this trend towards self-pollination in *Moraea demissa, M. flavescens* (Goldblatt) Goldblatt, and *M. pallida* (Baker) Goldblatt ($n = 4$ cytotype) as these species form *Oenothera*-type complex heterozygotes with rings of chromosomes at meiosis (Goldblatt 1980, 1981). The reproductive biology of these complex heterozygotes has not, however, received comprehensive study.

Pollination Trends in Selected Genera

Direct observations and/or literature on pollination systems in the genera *Aristea, Babiana, Duthiastrum, Ferraria, Hesperantha, Melasphaerula, Romulea,* and *Sparaxis* were lacking or limited at the time that we completed our first review (Bernhardt and Goldblatt 2000). Recent studies expand information on floral evolution in all these genera.

Aristea.—With some 50 species of sub-Saharan Africa and Madagascar, this is one of the most florally conservative genera in the family. All but six species have moderate-sized blue, rotate flowers with a vestigial perianth tube and exserted, yellow anthers. The flowers produce no nectar and are essentially pollen flowers. Observations on selected species (Goldblatt and Manning 1997*a*) show the flowers are visited by a range of female bees in the families Andrenidae, Apidae, and Halitidae that collect pollen for offspring. Five species, all of the southwestern Cape, South Africa, have larger flowers with dark markings on the tepals and enlarged, orange anthers, and are visited exclusively by hopliine beetles (Goldblatt and Manning 1997*b*). The white- or pale blue-flowered *A. spiralis* (L. f.) Ker Gawl., has perigonal nectaries, well-exserted anthers and is pollinated mainly by long-proboscid, *Philoliche rostrata* (Johnson 1992). We regard the majority of *Aristea* species as bee-pollinated with anthers dependent on active contact (Table 1) with fecund female bees and neuter *Apis* workers foraging for pollen. An additional four species endemic to Madagascar may also be exceptions to the rule as they have porose anthers (Goldblatt 1991) indicative of buzz pollination as treated in Tables 1 and 3.

Babiana.—Currently believed to comprise some 86 species (Goldblatt and Manning in press), this genus includes examples of all major pollination syndromes recorded in Iridaceae as described above (Table 1). Bee pollination subdivides into two discrete modes with the *B. ambigua* (Roem. & Schult.) G. J. Lewis group consisting of bilaterally symmetrical, nectariferous species pollinated by nectar-collecting anthophorine bees and *Apis* workers (passive contact). In contrast, the *B. villosula* Ker Gawl. ex Steud. group consists of four, radially symmetrical, nectar-poor species (Table 2) in which the anthers are scraped actively by *Apis mellifera* after nectar is sampled briefly. Variation in perianth tube length, scent production, and perianth pigmentation among species with bilaterally symmetrical flowers in this genus result in pollination by either anthophorines, long-proboscid flies, settling moths, or passerine birds. A few species that have nectarless and odorless, radially symmetric flowers with contrasting central markings or enlarged, blackish stamens (unusual in Iridaceae) are visited by hopliine beetles, as above. Comparing taxonomic relationships as currently understood (Goldblatt and Manning in press) with pollination systems, these authors estimate that a minimum of 14 shifts in pollination systems have occurred in this genus.

Duthiastrum.—This monotypic genus of central southern Africa is acaulescent and has an extended perianth tube. Floral examination (Manning pers. comm.) shows a tube tightly enclosing the style. The tube evidently serves only to raise the flower above the ground. The flowers are nectarless and offer only pollen to foragers. Female halictid bees have been captured while harvesting pollen.

Ferraria.—Wasp pollination and sapromyiophily (pollination by dung, carrion, and flesh flies) in *Ferraria,* a genus of ca. 14 species, has been discussed above. Field observations of *Ferraria ferrariola* (Jacq.) Willd. show it is pollinated by large-bodied, long-tongued anthophorine bees and *Apis* workers. The flowers have a relatively deep floral cup, a sweet spicy odor, and they secrete nectar of 28–35% sucrose equivalents. This concentration is far lower than the >50% sucrose equivalents of the fly-pollinated species, but much higher than the 4–9% in wasp-pollinated species (Goldblatt and Manning unpubl. data). Flowers of *F. ferrariola* resemble those of allied *Moraea* spp. in that the outer tepals are larger than the inner and bear nectar guides, while the inner tepals are somewhat reflexed. Consequently, flowers of *F. ferrariola* resemble the meranthium of three gullet-like units expressed in *Moraea.* At the present time, *Ferraria macrochlamys* (Baker) Goldblatt & J. C. Manning and *F. uncinata* Sweet show modes of floral presentation that do not readily suggest any of the pollination systems reported thus far in Iridaceae. We await novel observations of pollinator activity for both species.

Hesperantha.—This genus, with 79 weakly protandrous species, is pollinated by hairy scarabs, or long-proboscid flies, or large butterflies, or a combination of large-bodied, long-tongued bees and nocturnal moths (as discussed above), or by moths exclusively (Goldblatt et al. 2004*b*). More generalist systems incorporate bees with flies in the genus *Prosoeca,* as well as hairy scarabs. Flowers in this genus are, with one exception, radially symmetrical and their pollination systems appear to be determined by variation in only four characters. These are: (1) floral tube length correlating directly with the volume and concentration of nectar secretion, (2) the presence or absence of scent, (3) perianth colors, and (4) the time of day at which tepals open and close (Goldblatt et al. 2004*b*). Apparent pollination-by-deceit in nectarless, long-proboscid fly flowers of *H. pubinervia* Hilliard & B. L. Burtt and *H. scopulosa* Hilliard & B. L. Burtt is discussed above.

Romulea.—With 75 species in sub-Saharan Africa (Manning and Goldblatt 2001), this genus has radially symmetrical flowers exclusively, and both floral architecture and flowering patterns remain conservative. Therefore, it is not surprising that only three major pollination systems are expressed (Table 1). Pollination by bees (representing four native families) emphasizes foraging for pollen, as nectar production is usually too low to measure for volume or concentration. A second group is pollinated by hopliine scarabs, while the third depends on long-proboscid flies in the Nemestrinidae (Goldblatt et al. 2002). Differences between pollination systems in this genus emphasize differences between nectar secretion (Table 2), perianth pigmentation, and the relative length of the floral tube. Scent is sometimes found in species pollinated by pollen-collecting female and worker bees, but is otherwise absent in *Romulea* flowers.

Sparaxis.—With only 15 species, this genus expresses more variation in floral symmetry than the more speciose, *Romulea. Sparaxis* species with bilaterally symmetrical flowers are pollinated by nectar-foraging bees or by the long-proboscid fly, *Prosoeca peringueyi* (Table 1). *Sparaxis galeata* (Jacq.) Sweet, which has bilaterally symmetrical flowers, once thought to be an example of pollination-by-deceit, does, in fact, secrete nectar and is pollinated by large-bodied anthophorine bees (P. Goldblatt unpubl. data). The remaining species have a radially symmetrical perianth (the stamens and style are unilateral) or their flowers are fully radially symmetric with stamens and style symmetrical, have variable pigmentation patterns, and have a relatively narrow floral tube that secretes only trace amounts of nectar (Table 2). These remaining species have either a generalist mode of pollination, that is, they are pollinated by a combination of short-tongued, pollen-collecting female bees, *Apis mellifera* workers, and hopliine beetles. A second series is pollinated predominantly by hopliine beetles, sometimes complemented by visits by tabanid flies with short probosces (Goldblatt et al. 2000*b*).

DISCUSSION

The Relevance of Pollen Load Analyses

The bibionid fly-pollinated, monotypic genus *Melasphaerula* and the wasp-pollinated species in the genus *Ferraria* provide the only current examples of taxa in which all pollinators carried "pure" loads of host plant pollen exclusively. All other ongoing studies continue to confirm the previous review by Bernhardt and Goldblatt (2000) that the flowers of Iridaceae native to sub-Saharan Africa are pollinated by polyphagic animals and/or polylectic bees. In all other genera studied thus far, the majority of individuals of any insect species collected while foraging on the flowers of Iridaceae carried mixed loads of pollen, polyads, and pollinia from co-blooming taxa. Birds and all insects have been observed foraging for nectar, or pollen, or pollen and nectar on suitable co-blooming taxa when these were available. Pollen load analyses of vectors collected on flowers of Iridaceae imply the "inequality" of co-adaptation. That is, many species of African Iridaceae are dependent on remarkably few pollinator species and some flowers are pollinated by only a single animal species. In contrast, all evidence available to date indicates that no flower-visiting insect or bird is dependent on the floral rewards produced by a solitary plant species within Iridaceae. For example, *Prosoeca peringueyi* is the only known pollinator of some 25 species including *Babiana curviscapa* G. J. Lewis, *B. dregei* Baker, *Lapeirousia dolomitica* Dinter, *L. silenoides* (Jacq.) Ker Gawl., and *Tritonia marlothii* M. P. de Vos. Furthermore, *Babiana praemorsa* Goldblatt & J. C. Manning, *Lapeirousia oreogena,* and *Romulea hantamensis* (Diels) Goldblatt, and just a few more species depend solely on *Prosoeca* sp. nov.! In contrast, each species of long-proboscid fly has been documented taking nectar from numerous co-blooming species. It is common for a sub-Saharan species in Iridaceae to share its pollinator(s) with both other co-blooming species in Iridaceae as well as many other species in several unrelated families (see Goldblatt and Manning 1999; Goldblatt et al. 1995, 1998*a*, *b*, 1999, 2000*a*, *b*, 2002).

The overwhelming presence of mixed pollen loads on dominant pollen vectors provides the most compelling evidence for speciation following character displacement events (sensu Futuyma 1986). It is entirely clear, for example, that systems in which one or two animal species (e.g., long-proboscid flies) are the only pollinators of dozens of co-blooming angiosperm species reflects a trend towards asymmetrical coevolution (sensu Lunau 2004). These often unrelated plant species (see Goldblatt et al. 1998*a*) are far more dependent on relatively few animal species for pollen dispersal than the obviously polylectic/polyphagic animal is dependent on any single plant species for edible, life-sustaining rewards (Goldblatt and Manning 1999). Several plant species must be involved in some degree of competition for this limited pollinator resource ultimately provoking pollinator shifts due to unsuccessful competition with a co-blooming species due to the selective foraging behavior of the polyphagic pollinator. Character displacement following protracted competition would be particularly important (and rapid) if the species of pollinator has a naturally low population density.

Predictable Pollinator Shifts vs. Phylogenetic Constraints

We estimate that over 92% of species of Iridaceae of sub-Saharan Africa are pollinated primarily by insects representing at least one species in the orders Hymenoptera, Coleoptera, and Diptera. Of these, over 61% depend (at least,

in part) on bees or wasps (Hymenoptera), 14% on hairy scarab beetles (Coleoptera), and 13% on true flies (Diptera) to effect pollen dispersal. This estimation is based on a combination of the known pollination systems described and published for individual species and our current predictions of pollination systems for, as yet, unstudied species based on comparative analyses of entire suites of floral characters.

Pollinator systems exploiting bees are expected to be predominant for three overlapping reasons. First, bees are the dominant pollen vectors on this planet. Second, the bee-fauna of southern Africa give representatives of Iridaceae access to diverse foragers in different bee families with widely varying body sizes, proboscis lengths, and foraging behaviors. Third, bees and masarine wasps are the only insects known to collect pollen to feed their offspring. However, bees foraging exclusively for their offspring visit a different range of floral forms compared to bees foraging exclusively for nectar to feed themselves and/or other winged adults in the same hive or nest. Within the sub-Saharan African Iridaceae, it is easy to see a diverging trend in which nectariferous species with bilabiate flowers and concealed anthers occur within the same genus as nectar-poor (or nectarless) flowers with radially symmetrical flowers and prominently displayed anthers (e.g., *Gladiolus, Moraea*).

Pollinator shifts in Iridaceae work on a similar program of radiation for fly-pollinated systems. Representatives of seven fly families, with at least one flower-visiting species, are exploited by African Iridaceae. Fly foraging habits coupled with an astonishing variation in proboscis length among native dipterans show extremes that surpass even the Hymenoptera. In particular, hypermorphosis of the proboscis in the Nemestrinidae and Tabanidae for nectar-foraging appears to be strikingly well developed in southern Africa and this trend in fly evolution is regularly exploited by other angiosperm families that bloom with Iridaceae (Goldblatt and Manning 1999, and see above).

In contrast, the estimated 125 species pollinated, in part, or exclusively by beetles represent a quite different trend. Virtually all beetle species associated with successful dispersal of pollen of flowers in the Iridaceae of southern Africa belong to the same family and subtribe, Scarabaeidae: Hopliini (Goldblatt et al. 1998*a*). However, the "hairy scarabs" identified in these studies represent 15 genera and over 45 species at last count (see Goldblatt et al. 1998*a*, 2000*a, b*, 2002; H. Dombrow pers. comm., unpubl. data). It is most important to note that there are few examples of a single species in Iridaceae pollinated exclusively by a single species of beetle. One notable exception is the beetle, *Clania glenlyonensis* Dombrow, the only hopliine reported to pollinate both *Romulea monadelpha* (Sweet) Baker and *Hesperantha vaginata* (Sweet) Goldblatt. Floral modifications do not limit these two sympatric and co-blooming species to a solitary, pollen vector. Rather, both plant species are restricted to a distinctive soil type, as is their beetle pollinator (Goldblatt et al. 2002, 2004*b*). Therefore, we must conclude that most beetle species and the plants they pollinate most probably reflect coincidental and overlapping patterns of both local and seasonal distribution instead of highly specialized examples of co-adaptation. It is true that pigmentation patterns are quite variable in these beetle-pollinated species, but there is still little experimental evidence that one color pattern is more attractive to one genus or species of hairy scarab than a second pattern (Goldblatt et al. 1998*a*).

Hairy scarab pollination in Iridaceae remains the second most common mode of pollination in southern Africa because these pollen vectors are so numerous during flowering peaks and are interchangeable regardless of which beetle species dominates which site. Note that flowers pollinated by hairy scarabs are almost always radially symmetrical and form shallow bowls or salvers. The tepals often have sharply contrasting patterns of pigmentation (the famous "beetle marks"), most lack discernible scents, and produce only minute quantities of nectar, if they produce any nectar at all (Table 2). We suggest that the evolutionary "investment" required for the exploitation of hairy scarabs as pollinators may be far "cheaper" than pollination by most flower flies and many bees demanding nectar for their services and/or scent cues to locate flowers. As these beetles feed primarily on pollen as adults and lack elongated mouthparts, plants do not need to invest resources in the construction of either long floral tubes or complex bilaterally symmetrical perianths. It is not surprising then to learn that beetle pollination has evolved independently in at least one species in 12 of the 23 genera under consideration (Table 1) and it is exploited extensively in two large genera, *Ixia* and *Moraea.* Other examples of parallel and convergent evolution of hairy scarab pollination occur commonly in other families of both monocots and eudicots in southern Africa (Goldblatt et al. 1998*a*).

When we first reviewed pollination systems in the Iridaceae of southern Africa alone (Bernhardt and Goldblatt 2000) we concluded that the unusually high diversity of these pollination systems within a large genus reflected the primary consequence of adaptive radiation or (to a lesser extent) character displacement. That is, new species often evolved as the pollination systems of ancestral stock diversified and shifted and the biggest genera within this family reflected this evolutionary trend. For example, while pollination by large-bodied, nectar drinking bees is the dominant pollination system in southern African *Gladiolus,* with 87 out of 165 species expressing this system, another eight pollination systems are recorded for the remaining species in the genus. Likewise, the same mode of bee pollination dominates *Moraea,* with 108 out of 195 species, but four other pollination systems are also present within the lineage. Conversely, there are only three species each in the genera *Chasmanthe* and *Klattia* and all six species are bird pollinated. The ten *Nivenia* species have only two distinct pollination systems (Table 1).

We now realize that our hypothesis was somewhat simplistic and we recognize that adaptive radiation and/or character displacement alone is insufficient to trigger a cascade of pollination systems resulting in the multiplication of dozens of new species. Why? First of all, because some rather small genera also exhibit diverse pollination systems without the "by- product" of many species. For example, five pollination systems are found in *Sparaxis* (15 spp.) and three occur in *Crocosmia* with only eight species (Table 1). More important, some genera are species rich yet certain pollination systems remain absent in the genus although the same system is common in smaller genera. Note that pollination by birds, large butterflies, long-proboscid flies, and hawkmoths does not occur in *Moraea,* the second largest genus

of Iridaceae in sub-Saharan Africa. Only one species in *Gladiolus* is pollinated in part by hairy scarabs. There is no evidence of pollination by carrion or dung flies, wasps or oil-collecting bees in *Gladiolus,* although it remains the largest genus in the region. If repeated diversification of pollination mechanisms is the natural consequence of adaptive radiation within a lineage belonging to the Iridaceae of southern Africa, then at least one bird-pollinated species should be predicted for each genus containing >40 species. Instead bird pollination appears to be absent in *Aristea* (50 spp.), *Ixia* (52 spp.), *Lapeirousia* (41 spp.), and *Romulea* (75 spp.). This glaring absence traps us within an untestable hypothesis in which we are forced to invoke a history of selective extinction wiping out all bird-pollinated species in four genera. The coincidence is unbelievable.

Certainly there is continued merit in regarding the radiation/character displacement of pollination mechanisms as one of the most important aspects driving such intense speciation within this family in southern Africa. The problem is that it cannot always explain limited pollinator shifts within the same lineage. Consider how some modes of floral presentation overlap even though the main pollinators are unrelated. For example, red or orange pigmentation is characteristic of most species pollinated by birds (Goldblatt et al. 1999). However, these colors are not restricted to bird-pollinated systems in Iridaceae. The incorporation of some crimson to orange color patterns is also present in some beetle-, large butterfly- and even some long-proboscid fly-pollinated systems (Bernhardt and Goldblatt 2000). Other important floral characters such as sucrose-rich nectars, a bilaterally symmetrical perianth, elongated floral tubes, and sweet fragrances are shared across several pollination systems. It is this inheritance of whole suites of characters within the same lineage that may ultimately define the diversity of pollinator shifts.

Therefore, adaptive radiation and/or character displacement within a lineage should always be considered in conjunction with phylogenetic constraints. Some pollination systems fail to shift within a lineage because of the simple evolutionary history of inherited architecture. The absence of pollination systems favoring vectors with the longest mouthparts in the genera *Moraea* and *Ferraria* are based obviously on two interrelated constraints. These genera have free tepals and exhibit variations on the typical "meranthium" or *Iris*-type flower (see Bernhardt and Goldblatt 2000). The meranthium flower as expressed in sub-Saharan Africa appears incapable of evolving an elongated floral tube that is evidently necessary for competition with co-blooming species pollinated by birds, long-proboscid flies, hawkmoths, and large butterflies. Consequently, pollination in these two genera is restricted to pollinators with comparatively short mouthparts (beetles, wasps, some small-bodied bees, etc.) and/or insects that forage for pollen exclusively (beetles and female bees collecting pollen for offspring: Table 1).

Furthermore, a meranthium flower in *Moraea* is based on a "gullet system" (sensu Faegri and van der Pijl 1971) in which each style crest constitutes an upper lip and each opposed outer tepal limb forms a lower lip. Reduction of the style crests ultimately changes floral presentation (Goldblatt and Bernhardt 1999). Pollinator shifts occur within the genus when this reduction is associated with the loss of distinction between inner and outer tepal members and the development of a common bowl formed by the tepal claws. It is also associated with the suppression of nectar secretion and the development of beetle marks. Neither of these changes, however, effect overall perianth symmetry and all *Moraea* species in which style crests are reduced, or even absent, maintain a bowl-salver-shaped perianth now expressing simple radial symmetry. This must prevent the evolution of pollinator shifts in which passive anther contact (Table 2) depends on an animal probing the "throat" of a bilaterally symmetrical flower for nectar. Only with bilateral symmetry will the pollen vector be brushed or swabbed by the sexual organs that arch *below* the suberect or hooded uppermost tepal so common in some species of *Babiana, Gladiolus, Lapeirousia,* and other genera with this mode of architecture.

Therefore, pollinator shifts are predicted simply within a lineage consisting of a minimum of ten species provided that the lineage is derived from an ancestor that had a perianth united to form a true floral tube *and* some capacity for labile symmetry. Variation in tube length within a lineage permits shifts along a gradient of pollinators from short to long mouthparts. Variation in floral symmetry permits shifts along a continuum of pollinator bodies best exploited for either dorsal or ventral deposition of pollen.

We must emphasize, though, that variable tube length and labile floral symmetry represent two characters that are not always inherited together within a lineage of Crocoideae. While all genera in this subfamily have flowers in which the tepals are fused into a floral tube, some genera (e.g., *Freesia*) obviously lack the gene or gene sequence for converting bilateral symmetry (the ancestral state in most genera of the subfamily) into radial symmetry (see Goldblatt et al. 2006). Conversely, there are genera (*Ixia* and *Romulea*) of Crocoideae in which radial symmetry is ancestral. This explains why genera within Crocoideae with radially symmetrical flowers as the ancestral condition are more likely to exploit hopliine beetles or female bees that forage primarily for pollen. In contrast, while genera with ancestral, bilateral symmetry also exploit the same pollinators they form only a small fraction of plant species with such pollination systems within their respective genera.

Specialization vs. Phylogenetic Constraints

Sixteen relatively specialized modes of pollination are now described and inferred for ca. 900 species belonging to the Iridaceae of sub-Saharan Africa (Table 3). In this part of the world, Iridaceae show much the same predictable trend toward specialization as described in Asclepiadaceae, Orchidaceae (e.g., *Disa*), and Scrophulariaceae, which are distributed through the southern hemisphere (see Johnson and Steiner 2000). Therefore, there is still no obvious reason to alter the original observations of Bernhardt and Goldblatt (2000) that floral evolution within African members of Iridaceae reflects an ongoing trend toward *specialized* pollinator shifts.

What is most important, then, is that phylogenetic constraint within the sub-Saharan Iridaceae remains remarkably flexible regardless of the inherited floral bauplan. This family enjoys two modes of floral architecture and both modes require relatively few changes in morphology or biochem-

istry to shift pollination mechanisms. These shifts lead to the exploitation of quite different guilds of pollen vectors. The spectrum of pollinators possible in a flower inheriting the ancestral meranthium depends, in large part, on comparatively simple modifications to its stigmatic crests. Pollinator shifts within species in Crocoideae revolve around equally minor changes to tepal lobes and variation in floral tube length. More important, in both floral forms the diversity and foraging behavior of pollinators to a single plant species depends ultimately on whether the flower contains functional nectar glands.

Finally, we ask, need we really, really continue this ultimately sterile argument as to whether generalization or specialization is more important in floral evolution? Wouldn't it be better if we addressed generalization/specialization on a lineage-by-lineage basis with greater respect to the distribution and geography of each lineage? Can we even judge whether a plant species exhibits a generalist or specialist mode of pollination until we all agree on which field and lab techniques provide superior levels of assessment? If we can develop acceptable techniques to measure degrees of coevolution the future of our discipline may ultimately lie with testing the hypotheses of Lunau (2004).

ACKNOWLEDGMENTS

We thank James Carpenter, American Museum of Natural History, and Scott Fitzgerald, Oregon State University, for providing wasp and March fly identifications, respectively. Fieldwork associated with this study was funded by National Geographic Society grants 7103-01 and 7316-02.

LITERATURE CITED

BAKER, H. G., AND I. BAKER. 1983. Floral nectar sugar constituents in relation to pollinator type, pp. 117–141. *In* C. E. Jones and R. J. Little [eds.], A handbook of experimental pollination biology. Van Nostrand-Reinhold, New York, USA.

———, AND ———. 1990. The predictive value of nectar chemistry to the recognition of pollinator types. *Israel J. Bot.* **39**:157–166.

BERNHARDT, P. 1996. Anther adaptations in animal pollination, pp. 192–220. *In* W. G. D'Arcy and R. C. Keating [eds.], The anther: form, function and phylogeny. Cambridge University Press, Cambridge, UK.

———, AND P. GOLDBLATT. 2000. The diversity of pollination mechanisms in the Iridaceae of southern Africa, pp. 301–308. *In* K. Wilson and D. A. Morrison [eds.], Monocots: systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.

FAEGRI, K., AND L. VAN DER PIJL. 1971. The principles of pollination ecology, Ed. 3. Pergamon Press, New York, USA. 291 p.

FUTUYMA, D. J. 1986. Evolutionary biology, Ed. 3. Sinauer Associates, Inc., Sunderland, Massachusetts, USA. 763 p.

GESS, F. W. 1997. Contributions to a knowledge of *Ceramius* Latreille, *Celonites* Latreille, *Jugurtia* Saussure and *Masarina* Richards in South Africa (Hymenoptera: Vespidae: Masarinae). *Journal of Hymenoptera Research* **6**: 36–74.

GESS, S. K., AND F. W. GESS. 1989. Flower visiting by massarid wasps in southern Africa (Hymenoptera: Vespoidea: Masaridae). *Ann. Cape Prov. Mus., Nat. Hist.* **18**: 95–134.

GOLDBLATT, P. 1980. Uneven diploid numbers and complex heterozygosity in *Homeria* (Iridaceae). *Syst. Bot.* **5**: 337–340.

———. 1981. Systematics and biology of *Homeria* (Iridaceae). *Ann. Missouri Bot. Gard.* **68**: 413–503.

———. 1987. Systematics of the southern African genus *Hexaglottis* (Iridaceae–Iridoideae). *Ann. Missouri Bot. Gard.* **74**: 542–569.

———. 1991. Iridaceae—Famille 45, Ed. 2, pp. 1–45. *In* Flore de Madagascar et des Comores. Muséum National d'Histoire Naturelle, Paris, France.

———, AND P. BERNHARDT. 1990. Pollination biology of *Nivenia* (Iridaceae) and the presence of heterostylous self-compatibility. *Israel J. Bot.* **39**: 93–112.

———, AND ———. 1999. Pollination mechanics of *Moraea* species (Iridaceae) with a staminal column. *Ann. Missouri Bot. Gard.* **86**: 47–56.

———, ———, AND J. C. MANNING. 1998*a*. Pollination of petaloid geophytes by monkey beetles (Scarabaeidae: Rutelinae: Hopliini) in southern Africa. *Ann. Missouri Bot. Gard.* **85**: 215–230.

———, ———, AND ———. 1999. Evidence of bird pollination in Iridaceae of southern Africa. *Adansonia* **21**: 25–40.

———, ———, AND ———. 2000*a*. Adaptive radiation of pollination mechanisms in *Ixia* (Iridaceae: Crocoideae). *Ann. Missouri Bot. Gard.* **87**: 564–577.

———, ———, AND ———. 2005*a*. Observations on the floral biology of *Melasphaerula* (Iridaceae: Crocoideae): is this monotypic genus pollinated by March flies (Diptera: Bibionidae)? *Ann. Missouri Bot. Gard.* **92**: 268–274.

———, ———, AND ———. 2005*b*. Pollination mechanisms in the African genus *Moraea* (Iridaceae: Iridoideae): floral divergence and adaptation for pollen vector variability. *Adansonia* **27**: 21–46.

———, T. J. DAVIES, J. C. MANNING, M. VAN DER BANK, AND V. SAVOLAINEN. 2006. Phylogeny of Iridaceae subfamily Crocoideae based on a combined multigene plastid DNA analysis, pp. 399–411. *In* J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: comparative biology and evolution (excluding Poales). Rancho Santa Ana Botanic Garden, Claremont, California, USA.

———, AND J. C. MANNING. 1997*a*. New species of *Aristea* (Iridaceae) from South Africa and notes on the taxonomy and pollination biology of section *Pseudaristea*. *Novon* **7**: 137–144.

———, AND ———. 1997*b*. New species of *Aristea* section *Racemosae* (Iridaceae) from the Cape Flora, South Africa. *Novon* **7**: 357–365.

———, AND ———. 1999. The long-proboscid fly pollination system in *Gladiolus* (Iridaceae). *Ann. Missouri Bot. Gard.* **86**: 758–774.

———, AND ———. 2000. The long-proboscid fly pollination system in southern Africa. *Ann. Missouri Bot. Gard.* **87**: 146–170.

———, AND ———. 2002. Evidence for moth and butterfly pollination in *Gladiolus* (Iridaceae: Crocoideae). *Ann. Missouri Bot. Gard.* **89**: 110–124.

———, AND ———. In press. A systematic revision of the southern African genus *Babiana* (Iridaceae: Crocoideae). *Strelitzia*.

———, ———, AND P. BERNHARDT. 1995. Pollination biology of *Lapeirousia* subgenus *Lapeirousia* (Iridaceae) in southern Africa: floral divergence and adaptation for long-tongued fly pollination. *Ann. Missouri Bot. Gard.* **82**: 517–534.

———, ———, AND ———. 1998*b*. Adaptive radiation of bee-pollinated *Gladiolus* species (Iridaceae) in southern Africa. *Ann. Missouri Bot. Gard.* **85**: 492–517.

———, ———, AND ———. 2000*b*. Adaptive radiation of pollination mechanisms in *Sparaxis* (Iridaceae: Ixioideae). *Adansonia* **22**: 57–70.

———, ———, AND ———. 2001. Radiation of pollination systems in *Gladiolus* (Iridaceae: Crocoideae) in southern Africa. *Ann. Missouri Bot. Gard.* **88**: 713–734.

———, ———, AND ———. 2002. Floral biology of *Romulea* (Iridaceae; Crocoideae): a progression from a generalist to a specialist system. *Adansonia* **24**: 243–262.

———, ———, AND G. DUNLOP. 2004*a*. *Crocosmia* and *Chasmanthe*. Timber Press, Portland, Oregon, USA. 219 p.

———, I. NANNI, P. BERNHARDT, AND J. C. MANNING. 2004*b*. Floral biology of *Hesperantha* (Iridaceae: Crocoideae): shifts in flower color and timing of floral opening and closing radically change the pollination system. *Ann. Missouri Bot. Gard.* **91**: 186–206.

JOHNSON, S. D. 1992. Plant–animal relationships, pp. 175–205. *In* R. M. Cowling [ed.], The ecology of fynbos. Oxford University Press, Cape Town, South Africa.

———, AND K. E. STEINER. 1994. Efficient pollination of the mass-flowering Cape orchid *Disa obtusa* Lindl. (Orchidaceae) by *Bibio turneri* Edwards (Diptera: Bibionidae). *African Entomology* **2**: 64–66.

———, AND ———. 2000. Generalization versus specialization in plant pollination systems. *Trends Ecol. Evol.* **15**: 140–143.

LUNAU, K. 2004. Adaptive radiation and coevolution—pollination biology case studies. *Organisms Diversity & Evolution* **4**: 207–224.

MANNING, J. C., AND P. GOLDBLATT. 2001. A synoptic review of *Romulea* (Iridaceae: Crocoideae) in sub-Saharan Africa, the Arabian Peninsula and Socotra, including new species, biological notes, and a new infrageneric classification. *Adansonia* **23**: 59–108.

———, AND ———. 2002. The pollination of *Tritoniopsis parviflora* (Iridaceae) by the oil-collecting bee *Rediviva gigas* (Hymenoptera; Melittidae): the first record of oil-secretion in African Iridaceae. *S. African J. Bot.* **68**: 171–176.

STEBBINS, G. L. 1970. Adaptive radiation of reproductive characteristics in angiosperms, Vol. 1. Pollination mechanisms. *Ann. Rev. Ecol. Syst.* **1**: 307–326.

STRUCK, M. 1997. Floral divergence and convergence in the genus *Pelargonium* (Geraniaceae) in southern Africa: ecological and evolutionary considerations. *Pl. Syst. Evol.* **208**: 71–97.

VOGEL, S. 1974. Ölblumen und ölsammelnde Bienen. *Trop. Subtrop. Pflanzenwelt.* **7**: 285–574.

WASER, N. M., K. CHITTKA, M. V. PRICE, N. M. WILLIAMS, AND J. OLLERTON. 1996. Generalization in pollination systems and why it matters. *Ecology* **77**: 1043–1060.