FLORAL BIOLOGY OF *HESPERANTHA* (IRIDACEAE: CROCOIDEAE): HOW MINOR SHIFTS IN FLORAL PRESENTATION CHANGE THE POLLINATION SYSTEM[1]

Peter Goldblatt,[2] *Ingrid Nänni,*[3] *Peter Bernhardt,*[4] *and John C. Manning*[5]

ABSTRACT

Field observations, floral dissections of a representative range of *Hesperantha* species, and pollen load analyses of insects captured on many of them indicate that flowers of this African genus are cross pollinated by a relatively broad range of insects. The pollination ecology of *Hesperantha* can be divided into four overlapping systems that exploit insects of four orders (Coleoptera, Diptera, Hymenoptera, and Lepidoptera). Species of the *H. falcata* type have erect or nodding, salver-shaped, strongly fragrant, white flowers that open in the mid to late afternoon and evening and are pollinated by long-tongued apid bees and/or noctuid moths. Species of the *H. pauciflora* type have a virtually identical floral morphology, but the perianth is yellow or pink to mauve or blue and the flowers are usually unscented and are open during the day, closing between midday and late afternoon, ca. 16:30 H. Flowers of this type are also pollinated by apid bees, but in the southern African winter-rainfall zone other effective pollinators include nemestrinid flies (*Prosoeca*) with relatively short prosboces and hopliine scarab beetles. In *H. latifolia* type flowers the perianth is pink to magenta or red (rarely pale yellow), odorless, opens during the day but has an elongate perianth tube exceeding 18 mm in length. These flowers are pollinated mainly by long-proboscid flies in the genera *Prosoeca* and *Stenobasipteron* (Nemestrinidae) or *Philoliche* (Tabanidae), but the red flowers of *H. coccinea* are pollinated by a guild of large butterflies including *Papilio* and the satyrid *Aeropetes*. Lastly, *H. vaginata* has odorless and nectarless, short-tubed yellow flowers, usually with contrasting dark markings, that open only during the day and are pollinated exclusively by the hopliine scarab beetle, *Clania glenlyonensis.* The taxonomic distribution of plant species with these pollination systems makes it clear that shifts in pollination systems have occurred repeatedly across *Hesperantha*, although floral morphology and nectar biochemistry are relatively conservative. Whether flowers are nocturnal, crepuscular, or diurnal, only four variables affect the floral ecology: length of the perianth tube, presence or absence of floral fragrance, timing of anthesis, and the closely associated trait of perianth color. Thus, species with pink, magenta, red, or yellow flowers close at night and are rarely fragrant, whereas those with white or pale yellow flowers are nearly always fragrant and either open late in the day or only at sunset and remain open for most of the night. Species show considerable variation in nectar volume and sugar concentration, closely correlated with pollination system, while two long-tubed species with floral characters typical of long-proboscid fly pollination produce no nectar and are inferred to be Batesian or guild mimics that achieve pollination by deception.

Key words: bees, floral ecology, *Hesperantha*, hopliine beetles, Iridaceae, long-proboscid flies, nectar, pollination systems, settling moths.

The radiation and diversification of the African Iridaceae depend to a greater or lesser extent on the plasticity of pollination mechanisms, and all the larger genera of the family exhibit a wide range of floral adaptations and correlated sets of insect or avian pollinators (Bernhardt & Goldblatt, 2000).

For example, *Lapeirousia* is pollinated by long-proboscid flies, or bees and butterflies, or moths (Goldblatt et al., 1995). *Romulea* exploits scarab beetles, pollen-collecting bees or, in at least two species, long-proboscid nemestrinid flies (Goldblatt et al., 1998a; Manning & Goldblatt, 1996, and unpub-

lished). The majority of species of *Gladiolus* appear to be pollinated primarily by nectar-feeding apid and anthophorine bees (Goldblatt et al., 1998b), but some red-flowered species are pollinated by the large butterfly *Aeropetes* (Johnson & Bond, 1994), while others are dependent on andrenid bees, a combination of bees and hopliine beetles (Goldblatt et al., 1998a), long-proboscid flies, moths, or birds (Goldblatt & Manning, 1998; Goldblatt et al., 1999, 2001).

Hesperantha, a mid-sized genus of subfamily Crocoideae (syn. Ixioideae), comprises approximately 80 species (Goldblatt, 1984, 1986, 1987, 1993, 2003; Hilliard & Burtt, 1986; Goldblatt & Manning, 1996) distributed from the southern tip of Africa through the eastern African mountains as far north as Ethiopia and Cameroon. Diversity is greatest in southern Africa, where there are two centers of diversity and regional endemism: the Drakensberg of South Africa and Lesotho; and the west coast and near interior of Northern Cape and Western Cape Provinces of South Africa. Compared with the approximately 260 species of *Gladiolus,* the 50 species each of *Ixia* or *Watsonia,* or the 40 species of *Lapeirousia, Hesperantha* species have a conservative floral morphology. The relatively small flowers (tepals typically 10–25 mm long, exceptionally to 37 mm) are radially symmetric, have subequal tepals, and are arranged in slender to compact spicate inflorescences. The flowers of most species have a symmetrical androecium and a style that diverges at the mouth of the floral tube into three long, spreading branches. Interspecific floral variation is restricted to perianth tube length and degree of curvature, perianth color (uniformly white to cream vs. various shades of pink to purple, or yellow, sometimes with dark markings), the presence or absence of fragrance, the type of floral odor, and the timing of anthesis (Goldblatt, 1984, 2003).

A particularly unusual aspect of floral variation within this genus is the close linking of floral pigmentation with the presence of floral odor and timing of anthesis. White- or cream-flowered species of the southern African winter-rainfall zone are crepuscular or nocturnal and produce a strong floral fragrance, whereas species with flowers of other colors, and the white-flowered species of eastern southern Africa, are typically odorless, at least to the human nose. Field studies of the pollination systems of a selection of *Hesperantha* species were undertaken to define and compare intrageneric trends in the evolution of pollination mechanisms and the function(s) of floral traits.

MATERIALS AND METHODS

INFLORESCENCE PHENOLOGY AND FLORAL LIFE SPAN

Direct observations are presented on 34 *Hesperantha* species made in the field from 1993 to 2002 (Table 1) and supplemented by living collections at Kirstenbosch Botanic Gardens, Cape Town, and the Missouri Botanical Garden, St. Louis. Observations were made in the southern spring, summer, or autumn at sites in southern Africa (August to April). Observations of insect foraging involved 4 to 10 hours per plant species (or occasionally more) and included recording of floral attractants (pigmentation, scent), rewards (nectar), the mode and timing of anthesis (opening of individual buds), daily phenology, anther dehiscence patterns, expansion of stigmatic lobes, the behavior of insects on the flower, and the taxonomic diversity of floral foragers. Floral scent was noted in the field and in cultivated plants. Scents too weak to be immediately discerned by the human nose were recorded after individual flowers were picked and placed in clean, lidded glass jars and stored in a warm place. The contents of each jar was smelled after a minimum of 60 minutes (Buchmann, 1983). Plant voucher specimens are deposited in the herbaria at the Missouri Botanical Garden (MO) and Kirstenbosch Botanic Gardens (NBG) (Table 1).

COMPATIBILITY

Compatibility relationships were examined in two species, *Hesperantha quadrangula* and *H. pallescens,* both maintained in the laboratory and isolated from possible pollinators. Fruit and seed set were compared in five hand-selfed flowers and five flowers crossed with pollen of another individual of the same species. In the Iridaceae hand-selfing of as few as five flowers is usually sufficient, as results are seldom mixed. Either all self crosses result in seed set or none do. Likewise, xenogamous crosses always succeed.

NECTAR ANALYSIS

Nectar volume measurements were taken primarily from unbagged flowers in the field, soon after they opened, reflecting both rates of secretion and depletion. To collect nectar, mature flowers were picked and nectar was withdrawn from the base of the perianth tube with 3 µl capillary tubes after separating the ovary from the perianth base. The percentage of sucrose equivalents in fresh nectar was measured in the field or laboratory using a Bellingham and Stanley hand-held refractometer (0–

Table 1.   Study sites and voucher information for *Hesperantha* species studied. Vouchers are housed at MO (Goldblatt & Manning) or at NBG (other collectors). All study sites are in South Africa.

Species	Study site	Voucher
H. acuta (Lichst. ex Roem. & Schult.) Ker Gawl.	Western Cape, foot of Vanrhyn's Pass	*Goldblatt & Manning 11070*
H. bachmannii Baker	Glenlyon, Nieuwoudtville	*Goldblatt & Nänni 11152*
H. baurii Baker	Free State, The Sentinel	*Goldblatt & Manning 11051*
H. brevicaulis (Baker) G. J. Lewis	Mpumalanga, God's Window	*Goldblatt 72*
H. coccinea (Backh. & Harv.) Goldblatt & J. C. Manning		
site 1	Mpumalanga, near Lunsklip falls	*Goldblatt s.n.* no voucher
site 2	KwaZulu-Natal, Karkloof	*Goldblatt & Nänni 11242*
site 3	KwaZulu-Natal, Highmoor	*Goldblatt & Nänni 11249*
H. cucullata Klatt	Northern Cape, Nieuwoudtville	*Goldblatt 3954*
H. erecta (Baker) Benth. ex Baker	Western Cape, Vredenburg	*Goldblatt & Manning 11084*
H. falcata (L. f.) Ker Gawl.		
site 1	Western Cape, near Darling	*Goldblatt & Nänni 11096*
site 2	Western Cape, Caledon, Drayton	*Goldblatt 11161*
H. fibrosa Baker	Western Cape, Fairfield, Napier	*Goldblatt & Nänni 10251*
H. flava G. J. Lewis	Western Cape, near Matjesfontein	*Goldblatt 6074*
H. flexuosa Klatt	Northern Cape, near Springbok	*Goldblatt & Porter 12086*
H. grandiflora G. J. Lewis	Free State, The Sentinel	*Goldblatt s.n.* no voucher
H. huttonii (Baker) Hilliard & Burtt	Eastern Cape, Kologha Forest	*Goldblatt & Porter 12007*
H. lactea Baker	KwaZulu-Natal, Inchanga	*Goldblatt & Nänni 11235*
H. latifolia (Klatt) M. P. de Vos	Northern Cape, Kamiesberg	*Goldblatt & Manning 9723*
H. leucantha Baker	Free State, The Sentinel	*Goldblatt & Nänni 11232*
H. luticola Goldblatt	Northern Cape, near Middelpos	*Goldblatt 6067*
H. marlothii R. C. Foster	Northern Cape, near Nieuwoudtville	*Goldblatt 11403*
H. oligantha (Diels) Goldblatt	Northern Cape, Hantamsberg	*Goldblatt & Manning 10043*
H. pallescens Goldblatt	Western Cape, Piekeniers Kloof	*Goldblatt & Nänni 11161*
H. pauciflora G. J. Lewis (pink flowers)		
site 1	Northern Cape, Oorlogskloof	*Goldblatt & Manning 9975*
site 2	Northern Cape, near Nieuwoudtville	*Goldblatt s.n.* no voucher
H. pauciflora (yellow flowers)	Northern Cape, Papkuilsfontein south of Nieuwoudtville	*Goldblatt 11102*
H. pilosa (L. f.) Ker Gawl. (blue flowers)	Northern Cape, Bokkeveld Mts.	*Goldblatt 6272*
H. pilosa (white flowers)		
site 1	Western Cape, Darling	*Goldblatt & Nänni 11162*
site 2	Western Cape, Viljoen's Pass	*Goldblatt 11113*
site 3	Western Cape, Rooisand, Bot River	*Goldblatt 11148*
H. pseudopilosa Goldblatt	Northern Cape, near Nieuwoudtville	*Goldblatt 11108*
H. pubinervia Hilliard	Free State, The Sentinel	*Goldblatt & Manning 11052*
H. quadrangula Goldblatt	Northern Cape, near Middelpos	*Goldblatt 11157*
H. radiata (Jacq.) Ker Gawl.		
site 1	Western Cape, Malmesbury	*Goldblatt s.n.* no voucher
site 2	Northern Cape, near Nieuwoudtville	*Goldblatt & Nänni 11104A*
H. rivulicola Goldblatt	Northern Cape, near Nieuwoudtville	*Goldblatt & Nänni 11104*
H. scopulosa Hilliard	Free State, The Sentinel	*Goldblatt & Manning 9856*
H. similis (N. E. Br.) R. C. Foster	Mpumalanga, Long Tom Pass	*Goldblatt & Manning 10480*
H. spicata (Burm. f.) Ker Gawl.	Western Cape, Malmesbury	*Goldblatt 11087B*
H. stenosiphon Goldblatt	Eastern Cape, Cathcart district	*Goldblatt & Porter 12995*
H. sufflava Goldblatt	Western Cape, Malmesbury	*Goldblatt & Nänni 11087*
H. vaginata (Sweet) Goldblatt	Northern Cape, Glenlyon Farm	*Goldblatt 4035*
H. woodii Baker	Eastern Cape, Naude's Nek	*Goldblatt & Manning 11067*

50%) from five or more individuals per population, unless fewer individuals were available. Additional nectar samples were dried on Whatman filter paper no. 1 and sent to B.-E. van Wyk, Rand Afrikaans University, Johannesburg, for HPLC nectar sugar analysis.

INSECT OBSERVATION AND POLLEN LOAD ANALYSES

Behavior of insects on *Hesperantha* flowers was carefully observed to see whether insects contacted anthers and stigmas while foraging. Insects observed probing the floral tube or brushing the anthers or stigmas were captured and killed in a jar using ethyl acetate fumes. Pollen was removed from insects after specimens were pinned. To prevent contamination of the body of an insect with pollen carried by another in the same jar, each insect was wrapped in tissue as soon as it was immobilized by jar fumes. Body length and proboscis length of insects was recorded from captured specimens. Night-flying moths are difficult to capture simply because darkness makes them difficult to locate. Use of flashlights covered with translucent red cellophane paper for illumination significantly assisted observation and capture. Capturing some insects (especially long-proboscid flies) at some sites appeared to reduce the population significantly, so we therefore killed as few of these insects as necessary to obtain specimens for identification and pollen load analysis.

Removal of pollen from an insect involved gently scraping pollen off the body with a dissecting needle (see Goldblatt et al., 1998a, b). The residue from needle probes was collected on glass slides and mounted in 1 to 2 drops of Calberla's fluid (Ogden et al., 1974). In the case of long-proboscid flies, which are large insects, sites of pollen deposition are often quite discrete for each plant visited, and pollen species can often be identified without recourse to microscopic examination due to pollen coloration and position. Pollen grains were identified microscopically by comparison with a temporary reference set of pollen grain slides made from plants flowering at study sites. *Hesperantha* pollen grains are distinguished from co-blooming species, other than members of Iridaceae subfamily Crocoideae, by their large size, perforate-scabrate exine, and monosulcate aperture with prominent 2-banded operculum (Goldblatt et al., 1991).

Insect specimens were identified by R. W. Brooks, University of Kansas (Apidae), H. Dombrow, Worms, Germany (Scarabaeidae), D. Kroon, Sasolburg, South Africa, and H. Kruger, Transvaal Museum, Pretoria (Lepidoptera—moths), J. C. Manning (Diptera, Lepidoptera—butterflies), and Kim E. Steiner, National Botanical Institute, Cape Town (Mellittidae, Scarabaeidae). Voucher specimens are deposited at the Snow Entomological Museum, Lawrence, Kansas.

RESULTS

INFLORESCENCE PHENOLOGY AND FLORAL LIFE SPAN

Most *Hesperantha* species have an erect inflorescence reaching a height of 5–30 cm, but a few species of rocky habitats and cliffs, including *H. brevicaulis* and *H. scopulosa,* have weak, drooping stems and a nodding spike (Fig. 1). Individuals produce one or, in some species, two or more, simple spicate inflorescences annually, and flowering is closely synchronized within the same species or population both seasonally and diurnally. Flower buds are arranged more or less helically along the spike (Goldblatt, 1984, 2003). In six species, including *H. flava, H. humilis,* and *H. latifolia,* the flowering stem is mostly or entirely subterranean so that the flowers are borne close to ground level (Fig. 1B). Flowering periods broadly subdivide into a spring season (August and September, or October in a few species) in the southern African winter-rainfall zone or a summer–autumn season (December to April) in the summer-rainfall zone (Table 2). This coincides with the period of optimal plant growth during or soon after the main rainy season for the geographical area. A few species of the summer-rainfall zone flower in early to late spring (Hilliard & Burtt, 1986), sometimes before foliage leaves have been produced, but for logistical reasons we did not study these early flowering species.

The pattern of flower buds opening on an inflorescence is acropetal. In all *Hesperantha* species a mature flower expands and closes again within 12 hours at specific times characteristic of the species or population. White, cream, or pale yellow flowers of the southern African winter-rainfall zone are fragrant (Table 2) and typically open in the mid to late afternoon or at sunset and close at specific times in the night, always before daylight (Table 3). Flowers of other colors, and white- to cream-flowered species of the summer-rainfall zone, are scentless (Table 2) and open either in the early morning (*H. ciliolata, H. pilosa* blue-flowered form, as well as most pink-flowered species of eastern southern Africa) and close soon after midday, or open after the middle of the day (*H. pauciflora*) and close before sunset (Table 3). The red flowers of *H. coccinea* open in the early morning and close shortly before sunset. Examples of perianth color and form, re-

Table 2.   Floral characteristics of *Hesperantha* species arranged according to flower type. Measurements of the perianth tube include the wider upper portion that accommodates the head of a long-tongued insect; + = presence, − = absence, trace = amount too little to measure volumetrically; salver = salverform. White-flowered populations of *H. falcata* and *H. pilosa* are listed in the first group, while yellow-flowered or blue-flowered populations respectively are included in the second group. Examples of flower color in *Hesperantha* species are available in Manning et al. (2002) and at http://www.mobot.org/MOBOT/Research/Hesperanthapollination.pdf.

Species	Flower shape	Flower color	Tube length mm	Scent	Nectar	Flowering time
Hesperantha falcata group						
H. acuta	salver	white	8–11	yes	+	Aug.–Sep.
H. bachmannii	nodding tube	white	8–10	yes	+	Aug.–Sep.
H. cucullata	salver	white	7–9	yes	+	Aug.–Sep.
H. erecta	salver	white	8–10	yes	+	July–Sep.
H. falcata (also see below)	salver	white	7–9	yes	+	Aug.–Sep.
H. flava	tube-salver	yellow	20–26	yes	+	June–July
H. flexuosa	salver	white	7–9	yes	+	Aug.–Sep.
H. marlothii	nodding tube	white	ca. 12	yes	+	July–Aug.
H. pilosa (also see below)	salver	white	9–10	yes	+	Aug.–Sep.
H. pseudopilosa	salver	white	8–10	yes	+	Aug.–Sep.
H. quadrangula	salver	white	ca. 3	yes	trace	Sep.
H. radiata	nodding tube	white to cream	10–12	yes	+	Aug.–Sep.
H. rivulicola	salver	white	9–11	yes	+	Aug.–Sep.
H. spicata	salver	white	4–5	yes	+	Aug.–Oct.
H. sufflava	salver	yellow	12–16	yes	+	July–Aug.
Hesperantha pauciflora group						
H. baurii	salver	pink	8–10	no	trace	Jan.–Feb.
H. ciliolata	salver	pink	4–5	yes	+	Sep.
H. falcata (also see above)	salver	yellow	7–8	no	?	Aug.–Sep.
H. fibrosa	salver	pink	7–9	no	+	Aug.–Sep.
H. humilis	tube-salver	pink	18–22	no	−	June–July
H. leucantha	salver	pale pink	10–15	no	+	Jan.–Feb.
H. lactea	salver	creamy yellow	7–8	no	+	Jan.–Feb.
H. luticola	tube-salver	white with large dark marks on the tepals	30–45	no	trace	July–Aug.
H. pauciflora	salver	pink to purple, or yellow	6–8	no	trace or +	Aug.–Sep.
H. pilosa (also see above)	salver	blue	7–9	no	+	Aug.–Sep.
H. similis	salver	pink	4–5	no	trace	Jan.–Feb.
Hesperantha latifolia group						
H. brevicaulis	tube-salver	pink	22–30	no	+	Mar.–Apr.
H. coccinea	tube-salver	red (or pink)	(25–)30–38	no	+	Dec.–May
H. grandiflora	tube-salver	pink, anthers brown	28–32	no	+	Jan.–Feb.
H. huttonii	tube-salver	pale pink	22–35	no	+	Feb.–Mar.
H. latifolia	tube-salver	purple	20–27	no	+	Aug.–Sep.
H. oligantha	tube-salver	purple	25–35	no	+	Sep.
H. pubinervia	tube-salver	salmon-pink	20–25	no	−	Jan.–Feb.
H. scopulosa	tube-salver	pink	32–42	no	−	Feb.–Mar.
H. stenosiphon	tube-salver	pink, anthers black	45–60	no	+	Feb.–Mar.
H. woodii	tube-salver	pink	33–40	no	+	Feb.–Mar.
Hesperantha vaginata group						
H. vaginata	cup	yellow with brown markings	5–7	no	−	Aug.–Sep.
Unplaced species						
H. pallescens	tube-salver	pale yellow	18–22	no	+	Sep.

Table 3.   Contrasted timing of floral opening and closing in selected *Hesperantha* species. Only species for which precise information is available are included, and data are for study populations only (as in Table 1). Timing varies within populations according to weather conditions, and other populations of the same species may have different opening and closing patterns. Flowers of *H. scopulosa* do not fully close and have the tepals fully expanded for all daylight hours and partially so at night. N/a = not assessed.

Species	Opening	Closing	Days open
White-, cream-, or pale yellow-flowered species			
H. bachmannii	16:00–16:30	6:30–7:00	4
H. cucullata	(15:00–)16:00–16:30	(19:00–)20:00–20:30	n/a
H. erecta	(14:00–)15:00–15:30	(17:00–)18:30–19:00	4–5
H. falcata	(12:30–)15:30–16:30 or 17:30–18:00	21:00–21:30 or after 2:00	4–5
H. flava	16:00–17:00	n/a	n/a
H. lactea	11:45–12:30	16:00–16:30	n/a
H. marlothii	17:00–17:30	4:00–4:30	n/a
H. pallescens	8:00–8:30	18:30–19:00	n/a
H. pilosa (white-flowered)	17:30–18:00	3:30–4:30	4
H. pseudopilosa	(15:00–)18:00–18:30	after 0:00	n/a
H. quadrangula	16:00–16:30	19:00–19:30	3–4
H. radiata	18:00–18:30	5:30–6:30	6–7
sample 2	17:00–17:30	5:30–6:00	n/a
H. rivulicola	16:15–16:45	after 0:00	n/a
H. spicata	18:00–18:30	0:00–0:30	4–5
H. sufflava	15:30–16:00	after 0:30	4–5
Pink-, blue-, or deep yellow-flowered species			
H. baurii	7:30–8:00 or 11:00–11:30	11:30–12:00 or 16:30–17:00	3–4
H. brevicaulis	ca. 11:00	n/a	n/a
H. coccinea	7:30–8:00	18:00–19:00	3–4
H. humilis	8:00–9:00	16:00–16:30	n/a
H. oligantha	n/a	14:00–14:30	n/a
H. pauciflora	(13:00–)14:00–14:30	17:00–17:30	n/a
H. pilosa (blue-flowered)	8:30–9:00	12:30–13:00	n/a
H. vaginata	14:30–15:00	16:30–17:00	n/a
H. woodii	9:00–9:30	14:00–14:30	n/a

produced in color, are available in Manning et al. (2002). Representative photographs of *Hesperantha* flowers are also posted at the following URL together with this article: http://www.mobot.org/MOBOT/Research/Hesperanthapollination.pdf.

A flower typically lasts four days before collapse of the perianth, but in a few species with a white perianth, flowers last six or seven days (e.g., *Hesperantha radiata, H. spicata*), yet maintain the pattern of opening and closing at specific times (Table 3). Flower buds on the same inflorescence open sequentially, usually one day apart; hence, there may be three or four flowers open at any time on an inflorescence for species with flowers lasting four days, but up to eight flowers open in species in which flowers last six or seven days. When flowers close, the tepals cloak the anthers and stigmas completely. Ambient temperature influences anthesis. On cold (< 15°C), heavily overcast, or misty days, flowers may not open completely for the entire day or the normal timing of opening may be delayed until conditions are more favorable. The only exception we have encountered is *H. scopulosa*, the flowers of which do not close completely, but the tepals half close at sunset, and re-open fully to become extended at 90° to the tube after 7:00 H the next morning.

Flowers of all species studied are weakly protandrous. The anthers dehisce longitudinally within one to three hours after the tepals of a new bud first unfold, but this depends to some extent on ambient temperature and humidity (see above) and anthers dehisce later in the day under wet-cool conditions. The three stylar arms, the adaxial surfaces of which comprise the stigmatic surfaces, are held erect when the flower first opens but they diverge later during the same day, in most species spreading outward below the erect or divergent an-

thers, coming to lie over the extended tepals. In all species the style divides at (or in a few species below) the mouth of the perianth tube into three long, slender arms (a generic synapomorphy for *Hesperantha,* see Goldblatt, 1984, 2003) that extend between the filaments. Open flowers are typically held erect to suberect with the tepals spreading horizontally with the stamens symmetrically disposed. Anthers are developmentally extrorse with loculicidal dehiscence, and the pollen adheres to the dehisced anther locules. The filaments twist slightly in the open flower so that the anthers come to face inward or upward, depending on whether they are held erect (most species with colored tepals), or are articulated on the filaments, each one lying horizontally, at right-angles to the filament (crepuscular or nocturnal species with white or cream tepals). Stamens and style branches are asymmetrically disposed and declinate in *H. grandiflora,* the only species in the genus with a zygomorphic flower.

Compatibility varies within the genus. Several species have been reported to be self-compatible (Goldblatt, 1984) following hand-mediated self-pollinations but with reduced fertility (*Hesperantha bachmannii, H. cucullata, H. falcata*). Mechanical autogamy without apparent reduction in fertility occurred in *H. acuta, H. erecta, H. latifolia,* and *H. pallescens* in the absence of pollinators. *Hesperantha pauciflora* and *H. radiata* failed to set seed following self-pollinations by hand. In the course of the present study, self-compatibility was established for *H. quadrangula* and confirmed for *H. pallescens* (Goldblatt, 1984).

NECTAR

Nectar glands, when present (Table 4), are septal, as they are in the entire subfamily Crocoideae (Goldblatt, 1990, 1991; Goldblatt & Manning, unpublished). Nectar is secreted from three minute pores at the top of the ovary (one per chamber) directly into the base of the perianth tube where the accumulated fluid is retained until removed by a foraging insect. In species with the lower part of the tube narrow and tightly enveloping the style, a small amount of nectar may be present in the upper part of the tube, presumably the result of capillary action. Measurable volumes of nectar are produced in most species (Table 4), and volume correlates with tube length. The long-tubed flowers of *Hesperantha coccinea* (tube 25–38 mm long) and *H. grandiflora* (tube 28–32 mm long) produced the most nectar (up to 4.1 µl in the latter in flowers undisturbed by insects—the perianth had not fully ex-

panded when nectar was measured), while flowers of short-tubed *H. baurii, H. falcata, H. fibrosa, H. pilosa, H. quadrangula,* and *H. radiata* produced small amounts of measurable fluid (< 1.0 µl of nectar). The smallest quantities of nectar are produced by *H. leucantha* and *H. baurii* (less than 0.1 µl in the last species). There is a negative correlation between the percentage of sugar solute in *Hesperantha* nectar and nectar volume. Thus, species that secrete the greatest amount of fluid tend to produce nectars lowest in dissolved sugars (e.g., *H. brevicaulis, H. coccinea, H. grandiflora,* and *H. woodii*), while *H. falcata, H. pilosa, H. radiata,* and *H. spicata* secrete less than 0.5 µl of fluid that contains 35% to 48% dissolved sugars. Among species that secrete less than 0.5 µl, *H. bachmannii* appears exceptional in having relatively dilute nectar, with a mean of 21.5% dissolved sugars.

Sugar analyses of *Hesperantha* flowers (Table 4) indicate that species examined for sugar composition offer nectars that are sucrose rich. White-flowered species with flowers open in the late afternoon and evening, e.g., *H. falcata, H. pilosa, H. radiata,* and *H. spicata,* have nectar of unusually high sugar concentrations, 40–50%, while *H. baurii* has nectar of 48% to > 50% sucrose equivalents. All the species with white flowers so far examined secrete nectar, although there are only trace amounts in *H. quadrangula,* but nectar presence or absence varies in species with flowers of other colors. The long-tubed flowers of *H. pubinervia* and *H. scopulosa* produce no nectar at all.

FLORAL PRESENTATION AND POLLINATION SYSTEMS

Four overlapping pollination systems can be recognized in *Hesperantha.* Comparative floral traits of the four main systems are summarized in Table 2. The pollination systems and associated floral traits do not necessarily reflect the natural relationships of species.

The Hesperantha falcata *Group*

In this group, of which *Hesperantha falcata* and *H. cucullata* are typical examples, the flowers are crepuscular or nocturnal and mostly white to cream or exceptionally pale yellow, and the perianth is salver-shaped with horizontally extended tepals (Figs. 1A, 2A) or in three species, nodding (Figs. 1D, 2B) with lightly reflexed tepals (*H. bachmannii, H. marlothii,* and *H. radiata*). The floral tube is cylindrical, expanding slightly near the apex, and hollow with a narrow, uniform diameter of about 1 mm. The tube typically contains nectar in the lower 1–3 mm. The perianth tube is usually slightly

Table 4.   Nectar properties of *Hesperantha* species that produce measurable quantities of nectar (see Table 2). SD = standard deviation, (n) = number of individuals sampled, Fru = fructose, Glu = glucose, n/a = not assessed. Nectar sugars were analyzed by B.-E. van Wyk (Rand Afrikaans University, Johannesburg, South Africa). Data marked with an asterisk are from Johnson and Bond (1994). For *H. acuta* and one population of *H. falcata*, nectar from three flowers was pooled to obtain sufficient nectar to register a refractometer reading.

Hesperantha species	Nectar (n)		% Nectar sugars			Mean Sucrose/ Glu + Fru (n)
	Volume μl	Mean % sucrose equivalents (±SD)	Fructose	Glucose	Sucrose	
H. acuta	0.4–0.8 (3)	36 (pooled sample)	n/a	n/a	n/a	n/a
H. bachmannii	0.2–0.4 (8)	21.5 (2.6)	n/a	n/a	n/a	n/a
H. baurii	trace to 0.1 (6)	49–>50	n/a	n/a	n/a	n/a
H. brevicaulis	1.0–1.6 (3)	19.3 (1.5)	n/a	n/a	n/a	n/a
H. coccinea						
site 1	2.4–3.7 (5)	20.8 (1.6)	n/a	n/a	n/a	n/a
site 2	2.2–2.9 (10)	15.4 (0.9)	n/a	n/a	n/a	n/a
site 3*	1.9 (19)	17.4 (n = 11)	42	43	15	0.18 (1)
H. cucullata	0.2–0.6 (8)	40.6 (3.7)	n/a	n/a	n/a	n/a
H. falcata						
site 1	0.3–0.5 (3)	32 (pooled sample)	39	38	23	0.27 (1)
site 2	0.2–0.5 (6)	36.2 (3.5)	n/a	n/a	n/a	n/a
H. fibrosa	0.3–0.4 (4)	21.3 (2.1)	24–25	15–28	47–61	1.17 (2)
H. grandiflora	2.8–4.1 (5)	14.8 (1.0)	n/a	n/a	n/a	n/a
H. huttonii	1.3–2.4 (8)	13.7 (1.6)	n/a	n/a	n/a	n/a
H. lactea	0.1–0.6 (10)	21.6 (3.6)	n/a	n/a	n/a	n/a
H. latifolia	0.7–1.1 (10)	28.5 (3.4)	23–29	24–30	41–53	0.94 (3)
H. leucantha	0.4–1.0 (4)	46.8 (1.0)	n/a	n/a	n/a	n/a
H. marlothii	1.4–2.2 (10)	35.9 (3.8)	n/a	n/a	n/a	n/a
H. oligantha	1.1–1.8 (5)	26.4 (3.9)	19–23	24–25	52–57	1.20 (2)
H. pallescens	0.8–1.2 (10)	35.5 (5.6)	n/a	n/a	n/a	n/a
H. pauciflora (pink flowers)	0.1–0.5 (5)	35.4 (1.7)	n/a	n/a	n/a	n/a
(yellow flowers)	0.6–0.7 (10)	23.5 (2.4)	n/a	n/a	n/a	n/a
H. pilosa (blue flowers)	0.2–0.4 (5)	44.2 (1.9)	n/a	n/a	n/a	n/a
(white flowers)	0.1–0.5 (10)	35.7 (3.5)	n/a	n/a	n/a	n/a
site 2	0.2–0.4 (3)	45.0 (6.1)	n/a	n/a	n/a	n/a
site 3	0.2–0.5 (6)	44.8 (2.7)	n/a	n/a	n/a	n/a
H. pseudopilosa	0.2–0.5 (2)	42.0–48.5	n/a	n/a	n/a	n/a
H. radiata						
site 1	0.2–0.4 (2)	n/a	11–20	16–20	60–73	1.86 (3)
site 2	0.2–0.5 (3)	42.4 (3.9)	n/a	n/a	n/a	n/a
H. rivulicola	0.2–0.5 (3)	48.0 (2.0)	n/a	n/a	n/a	n/a
H. spicata	0.2–0.5 (2)	42–45	n/a	n/a	n/a	n/a
H. stenosiphon	4.2–6.5 (11)	17.5 (2.0)	n/a	n/a	n/a	n/a
H. sufflava	0.4–1.2 (10)	28.0 (2.6)	n/a	n/a	n/a	n/a
H. woodii	1.2–1.8 (5)	18.1 (0.9)	n/a	n/a	n/a	n/a

shorter than the tepals, thus 7–16 mm long (Table 2) compared to tepals 12–16 mm long, but the tube is half again as long as the tepals in *H. flava*, 20–26 mm long, compared with tepals up to 16 mm long.

Almost all white- to pale yellow-flowered species of the southern African winter-rainfall zone are crepuscular or fully nocturnal (Table 3). The perianth opens in the late afternoon, typically after 16:00 H or at sunset, and closes before sunrise. *Hesperantha*

pauciflora is an exception. A rare, pale yellow-flowered form of this otherwise pink-flowered species (Goldblatt, 2003) has the tepals opening soon after midday and closing before sunset. *Hesperantha quadrangula* is unusual: its white flowers have an unusually short perianth tube, 2–3 mm, compared to the tepals, 9–12 mm long, and they open at ca. 16:00 H and close shortly after sunset but before dark, ca. 19:00 H. The widespread and common *H. falcata* is notable for the varied times that flowers

Figure 1. Growth forms and plant habit in *Hesperantha*. —A. *H. acuta.* —B. *H. humilis.* —C. *H. oligantha.* —D. *H. radiata.* Scale bar = 10 mm for A, B, and D; 15 mm for C. (Drawn by Margo Branch, Cape Town.)

of different populations open, some opening as early as 16:00 H, and others after 17:30 H, but in all populations we examined, the flowers remain open after 21:00 H. In *H. erecta,* the perianth opens at ca. 15:00 H.

The eastern southern African *Hesperantha lac-* *tea, H. hygrophila* Hilliard & Burtt, *H. inconspicua* (Schltr.) G. J. Lewis, and *H. rupestris* N. E. Br. ex R. C. Foster (the latter three not studied here) have unscented, diurnal flowers with a white to cream perianth that are open for only a portion of the day and close fully before sunset, between midday and
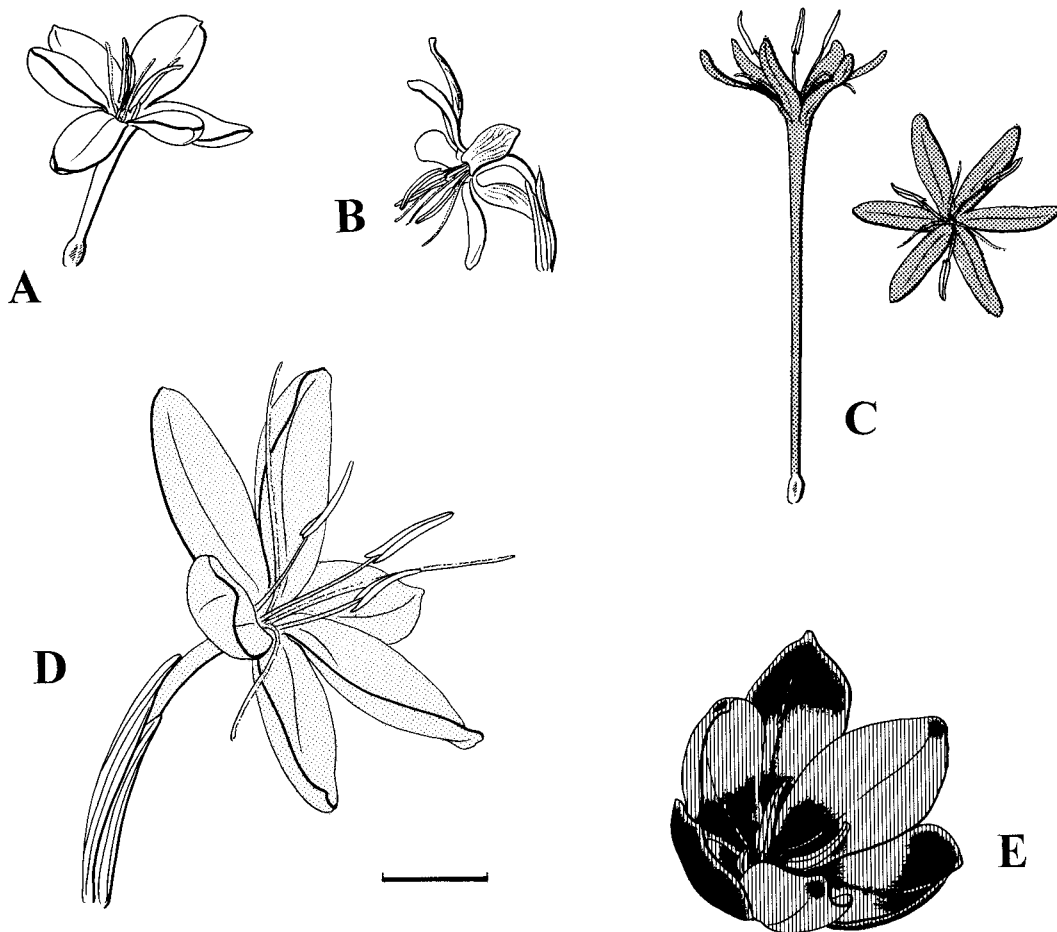
Figure. 2.   Perianth types in *Hesperantha*. —A. *H. sufflava*. —B. *H. radiata*. —C. *H. oligantha*. —D. *H. coccinea*. —E. *H. vaginata*. Scale bar = 10 mm. Shading code: dark stippling = purple (*H. oligantha*); light stippling = red (*H. coccinea*); vertical hatching = yellow; and solid black = brown (*H. vaginata*). Drawn by John Manning.

late afternoon depending on the species (Hilliard & Burtt, 1986; Goldblatt, 2003). Thus in all respects except perianth color they resemble more closely species of the next group, the *H. pauciflora* group.

When open, the flowers of species belonging to the *Hesperantha falcata* group produce a strong, sweet fragrance that is variable between, and sometimes within, species. Scents range from light rose (*H. quadrangula*, *H. rivulicola*) to jasmine or frangipani (*Plumeria*) (*H. cucullata*, *H. falcata*—some populations; *H. flexuosa*, *H. pilosa*—some populations), narcissus (*H. spicata*), acrid-musk (*H. erecta*, *H. falcata*—some populations; *H. pilosa*—some populations; *H. sufflava*), or sweet with a strong clove component (*H. marlothii*, *H. radiata*).

Hesperantha cucullata, *H. pilosa*, *H. quadrangula*, *H. rivulicola*, *H. sufflava*, and sometimes *H. falcata* are actively visited by large-bodied apid

bees (Tables 5, 6) with probosces 3–10 mm long. Bees forage for both pollen and nectar soon after the flowers open in the late afternoon. The white flowers are conspicuous in the late afternoon light, and *Anthophora* species or *Apis mellifera* can often be seen visiting the flowers of these species. Small settling nocturnal moths, mostly noctuids, and most commonly *Heliotis armigera*, but also species of Adelidae, Drepanogynidae, Geometridae, and Pyralidae (Tables 5, 6), with probosces 4–12 mm long are common and active at or after sunset and in the early evening in the southern African winter-rainfall zone, and regularly visit flowers of all the species we observed for pollinators after sunset (*H. bachmannii*, *H. cucullata*, *H. falcata*, *H. marlothii*, *H. pilosa*, *H. pseudospicata*, *H. radiata*, and *H. rivulicola*). Both bees and moths are polylectic foragers, and individual bees were found to carry the pollen of co-blooming species (Table 6), including

Table 5. Length of mouth parts of insects captured on *Hesperantha* flowers, with perianth tube lengths. Measurements are ranges for the insect or plant populations studied.

Insect species	Mouth part mm (n)	Plants on which insect captured	Tube length mm
Diptera			
Prosoeca ganglbauri	27–30 (4)	*H. grandiflora, H. scopulosa*	28–42
P. ganglbauri	28–32 (4)	*H. woodii*	35–38
P. peringueyi	20–25 (3)	*H. latifolia*	15–25
P. sp. nov. 2	ca. 9 (2)	*H. pauciflora*	6–8
Stenobasipteron wiedemannii	19–23 (3)	*H. huttonii*	25–35
Hymenoptera			
Amegilla capensis	9–10 (3)	*H. baurii*	8–10
Anthophora diversipes	6.5–8 (4)	*H. cucullata, H. pauciflora, H. pilosa, H. rivulicola,*	6–12
		H. sufflava	12–16
Apis mellifera	3–4 (10)	*H. baurii, H. cucullata, H. falcata*	7–10
Lepidoptera [butterflies]			
Aeropetes	ca. 30 (1)	*H. coccinea*	30–38
Papilio demodocus	ca. 25 (1)	*H. coccinea*	30–38
P. nireus	22 (1)	*H. coccinea*	30–38
Lepidoptera [moths]			
Agrotis segetum	ca. 11 (1)	*H. rivulicola*	8–11
Ceromitia sp.	11–12 (7)	*H. pseudopilosa, H. radiata, H. rivulicola*	8–12
Cucullia terensis	ca. 12 (3)	*H. cucullata, H. pilosa*	7–10
Drepanogynis sp.	ca. 10 (1)	*H. rivulicola*	8–11
D. dochmoleuca	ca. 7 (1)	*H. pilosa*	9–10
D. rufigrisea	ca. 11 (1)	*H. bachmannii*	8–10
Heliotis armigera	8–9 (6)	*H. bachmannii, H. cucullata, H. pseudopilosa, H. radiata*	8–12
Nomophila noctuella	5–7 (6)	*H. cucullata, H. pseudopilosa, H. radiata*	7–12
Perizoma artifex	ca. 4 (1)	*H. pilosa*	9–10
Xylopteryx arcuata	ca. 8 (2)	*H. cucullata*	7–9

Bulbinella (Asphodelaceae), *Lachenalia* (Hyacinthaceae), *Hermannia* (Malvaceae), and Iridaceae (including *Gladiolus, Moraea*) in their scopae or corbiculae and/or on various parts of their bodies. In contrast, only *Hesperantha* pollen was found on the bodies of captured moths except for one visiting *H. pilosa,* but as there were no other obvious night-flowering species at most of our study sites this is not surprising.

All moths captured while visiting *Hesperantha* flowers settled on the inflorescence and crawled over the flowers. They carried pollen on the underside of the wings, ventral part of the thorax, legs, and sometimes on the antennae and proboscis. One moth captured on *Cyphia bulbosa* (L.) P. J. Bergius (Campanulaceae) at our *H. pilosa* study site carried pollen of that species as well as that of *H. pilosa.* Pollen loads were light, often only a few grains being present. The bodies of moths are, however, poor surfaces for carrying pollen, and it is not surprising that after capture in a net and transfer to a killing bottle very little pollen remained on their bodies by the time they had been pinned and then examined. Moth activity was found to be at a maximum for the first hour and a half after sunset, thus until about 20:30 H. After this we noted few, if any, moth visits and we therefore did not continue our observations. It is possible that other moth species become active later, as noted by Johnson et al. (1993) for *Crassula fascicularis* Lam. (Crassulaceae), but flowers of most crepuscular or nocturnal *Hesperantha* species close before 1:00 H, exceptions being *H. marlothii, H. radiata,* and *H. rivulicola,* the flowers of which remain open until dawn or daylight.

The pollination by small settling moths in *Hesperantha* follows the pattern described by Johnson (1997) for species of the orchid genus *Satyrium.*

Johnson recorded a similar suite of moths visiting different species of that genus at night: *Heliotis armigera* and *Syngrapha circumflexa* on *S. bicorne* (L.) Thunb. and *Agrotis segetum* on *Satyrium ligulatum* Lindl. and *S. stenopetalum* Lindl. with the butterfly *Vanessa cardui* also visiting *S. ligulatum* during the day, a pattern paralleled in *H. rivulicola*. A high nectar sugar concentration of 40.1% was also noted for *S. stenopetalum,* which is comparable to the high nectar sugar concentrations we found in most settling moth-pollinated species of *Hesperantha*.

Those white-flowered species with flowers opening at or after sunset, including *Hesperantha flava, H. marlothii,* and *H. radiata,* have not been seen to be visited by bees. The long-tubed *H. flava* may receive visits from sphinx moths according to Vogel (1954), but while this is consistent with its long perianth tube (18–28 mm long), we assume that Vogel was only making a suggestion and did not observe sphinx moths visiting the species. Among the white-flowered species of the winter-rainfall zone *H. quadrangula* is exceptional in having flowers that close at about sunset, that is, before moths are normally active. Thus, although it has white flowers that open in the late afternoon, it is evidently not pollinated by moths.

The Hesperantha pauciflora *Group*

The *Hesperantha pauciflora* group (Table 2) includes the common eastern southern African *H. baurii,* its allies, *H. lactea, H. leucantha, H. similis,* and several more, the western Cape *H. pauciflora,* and western Karoo *H. humilis* (Fig. 1B). The perianth coloration is usually pink to purple, but blue or mauve in some populations of *H. pilosa* and in *H. ciliolata,* and cream to pale yellow in *H. lactea.* Floral structure in this group is virtually identical to that of the *H. falcata* group, but the flowers are typically scentless (Table 2) and the tepals unfold during the day, often in the morning, and close at midday or shortly thereafter (*H. baurii, H. pilosa*— blue form, *H. similis*), or in the early afternoon, then closing by 17.30 H (*H. pauciflora*). *Hesperantha ciliolata* is exceptional in having fragrant flowers that produce an unusual acrid, musky scent reminiscent of that produced by some southern African species of the orchid genera *Corycium* and *Pterygodium,* and differing markedly from the sweet odors of species of the *H. falcata* group. Flowers of the *H. pauciflora* group produce small quantities of nectar, mostly 0.1–0.3 μl in volume (Table 4). Flowers actively visited by bees may, however, contain no detectable nectar when sampled in the field. When

sampled later, after placing cut stems in water overnight, flowers yield nectar, indicating that visiting insects may have removed all available nectar during their foraging, or alternatively insufficient water was available to plants to allow nectar production.

Species in this group are pollinated primarily by large-bodied female anthophorine bees or worker honey bees foraging for pollen or nectar, or for both rewards. Bees land on the flower and brush both the anthers and stigma lobes as they crawl over the perianth while scraping pollen into their scopae or corbiculae. Most apid bees, *Amegilla, Anthophora,* and most *Apis mellifera* workers captured on *Hesperantha* flowers are polylectic foragers (Table 6), and individuals were found to carry the pollen of co-blooming Fabaceae, Asphodelaceae, Hyacinthaceae, Boraginaceae, and Iridaceae in their scopae or corbiculae and on various parts of their bodies. Perhaps significantly, however, almost half the *Apis mellifera* workers captured, 11 out of 26 individuals, carried pure loads of *Hesperantha* pollen, indicating temporary floral constancy, unlike other bees analyzed for their pollen loads (Table 6). Flowers of *H. pauciflora* are occasionally also visited by a relatively short-proboscid *Prosoeca* species, presently undescribed (Table 6), which behave much as anthophorine bees in search of nectar.

Species of this group may also be visited by hopliine beetles, but the significance of these beetles compared to bees visiting the same species is difficult to assess. Hopliine beetles often visit a range of plant species with the large, brightly colored flowers that are particularly suited to their activities (Picker & Midgely, 1996; Goldblatt et al., 1998b), which include assembly, competitive behavior, and copulation. Nevertheless, it may be best to regard species visited by both bees and hopliine beetles as exploiting both groups of pollinators.

The Hesperantha latifolia *Group (Table 2)*

The Namaqualand and western Karoo species, *Hesperantha latifolia* and *H. oligantha,* and the eastern southern African *H. brevicaulis, H. grandiflora, H. huttonii, H. scopulosa, H. stenosiphon,* and *H. woodii* exemplify the third pollination category (Figs. 1C, 2C). In these species the flowers are odorless, have an elongate perianth tube 20–60 mm long, and usually a pink to purple (rarely red) perianth. The tepals are shorter than the tube, mostly 15–25 mm long (exceptionally to 42 mm in *H. scopulosa* and to 38 mm in *H. grandiflora*), and spread horizontally, or are slightly cupped in *H. stenosiphon* and *H. woodii.* Exceptional in the group and genus, *H. grandiflora* has the tube sharply bent

Table 6.   Pollen load analysis of captured insects on *Hesperantha* species. Coleoptera: Scarabaeidae: *Anisochelus, Anisonyx, Clania.* Hymenoptera: Apidae: *Allodape, Amegilla, Anthophora, Apis.* Colletidae: *Scrapter.* Halictidae: *Patellapis.* Melittidae: *Rediviva.* Diptera: Nemestrinidae: *Prosoeca, Stenobasipteron.* Lepidoptera: Adelidae: *Ceromitia.* Drepanogynidae: *Drepanogynis.* Geometridae: *Perizoma, Xylopteryx.* Noctuidae: *Agrotis, Cucullia, Heliotis.* Nymphalidae: *Vanessa.* Pieridae: *Papilio.* Pyralidae: *Nomophila.* Satyridae: *Aeropetes.* Sphingidae: *Hippotion.* Data for *Hesperantha vaginata* are from Goldblatt et al. (1998b) and those for *H. latifolia* are from Manning and Goldblatt (1996). Site numbers refer to study sites as indicated in Table 1.

	Number of insects carrying pollen load(s)	
Plant and insect taxon	Pollen from host flower alone	Pollen from host flower plus other species
H. baurii		
site 1		
Amegilla capensis ♀	0	3
Patellapis sp. ♀	0	1
Rediviva nelii ♀	0	6
hopliine beetle 1	0	1
hopliine beetle 2[1]	3	3
site 2		
Apis mellifera	5	0
H. bachmannii		
Drepanogynis rufigrisea	1	0
Heliotis armigera	1	0
unidentified noctuid moth	1	0
H. brevicaulis		
Stenobasipteron wiedemannii	not captured	
H. coccinea		
site 2		
Papilio nireus	1	0
Papilio demodocus	1	0
site 3		
Aeropetes tulbaghia	1	0
H. cucullata		
Anthophora praecox ♀	0	1
A. schulzei 1 ♀ 1 ♂	0	2
Apis mellifera	3	0
Cucullia terensis	1	0
Heliotis armigera	4	0
Nomophila noctuella	3	0
Xylopteryx arcuata	2	0
H. erecta		
Apis mellifera	0	5
Anthophora rufidicaudis ♀	0	2
H. falcata		
site 1		
Apis mellifera	1	4
site 2		
(moths incl. *Heliotis armigera* seen but not captured)		
H. flexuosa		
Anthophora praecox ♀	0	2
Apis mellifera	0	2
H. grandiflora		
Prosoeca ganglbauri	0	3
H. huttonii		
Stenobasipteron wiedemannii[1]	0	3
H. lactea		
Allodape stellarum ♀	0	2
H. latifolia		
Prosoeca peringueyi	0	4

Table 6.   Continued.

Plant and insect taxon	Number of insects carrying pollen load(s)	
	Pollen from host flower alone	Pollen from host flower plus other species
H. luticola		
Apis mellifera	0	2
H. marlothii		
Cuculia terensis	1	0
(*Hippotion celerio* seen but not captured)		
H. pauciflora (pink flowers)		
site 1		
Apis mellifera	0	4
site 2		
Anisochelus inornatus[1]	2	3
Anthophora schulzei ♀	0	2
Prosoeca sp. nov.	0	2
(yellow flowers)		
Anisochelus inornatus	2	1
Anthophora diversipes ♀	0	1
Apis mellifera	2	0
H. pilosa (blue flowers)		
Apis mellifera	2	3
Anthophora schulzei ♀	0	1
Anthophora krugeri ♀	0	1
Anthophora diversipes ♀		
(white flowers)	0	1
Anthophora rufidicaudis ♀	0	2
Cucullia terensis	2	0
Drepanogynis dochmoleuca	1	0 (1 with no pollen)
Perizoma artifex	1	0
H. pseudopilosa		
Ceromitia sp.	2	0
Drepanogynis rufogrisea	1	0 (1 with no pollen)
Heliotis armigera	4	0 (5 with no pollen)
Heliotis scutuligera	1	1
Nomophila noctuella	4	0 (2 with no pollen)
(*Hippotion celerio* was captured but did not contact style branches or anthers and carried no *Hesperantha* pollen)		
H. quadrangula		
Apis mellifera	0	2
Anthophora diversipes ♀	0	2
Scrapter sp. indet. ♀	0	1
Anisonyx ignitus	0	1
H. radiata		
Ceromitia sp.	2	0
Heliotis armigera	1	0
Nomophila noctuella	1	0
H. rivulicola		
Anthophora diversipes ♀	0	4
Agrotis segetum	1	0
Ceromitia sp.	3	0 (1 with no pollen)
Drepanogynis sp.	1	0
(*Vanessa cardui* was not captured but individuals were seen to contact anthers and style branches on visits)		
H. scopulosa		
Prosoeca ganglbauri	0	3
H. similis		
Amegilla capensis ♀	0	2
H. stenosiphon		
Apis mellifera[1]	3	2

Table 6.   Continued.

| Plant and insect taxon | Number of insects carrying pollen load(s) | |
	Pollen from host flower alone	Pollen from host flower plus other species
H. sufflava		
Apis mellifera	0	2
Anthophora rufidicaudis ♀	0	2
Anthophora krugeri ♀	0	1
Anisonyx ditus	0	3
Scrapter sp. nov. ♀	0	2
Scrapter aff. *albitarsis* ♀	0	2
H. vaginata		
Clania glenlyonensis[2]	7	5
H. woodii		
Prosoeca ganglbauri	2	3
Total	74	105

[1] = more individuals seen but not captured.
[2] = *Lepisia* sp. of Goldblatt et al. (1998b).

near the apex so that the flowers face to the side, with the tepals held more or less vertically. The stamens and style branches of this species are unilateral with the anthers and style arms arching downward. Flowers of the *H. latifolia* group typically produce relatively large quantities of nectar (Table 4), mostly 1–4 μl in volume with concentrations ranging from 14.8 to 28.5% sucrose equivalents. Eastern southern African species have unusually low nectar concentrations, less than 21% sucrose equivalents and with a mean as low as 14.8% in *H. grandiflora* and 13.7% in *H. huttonii.* The flowers of *H. scopulosa* lack nectar, as do those of *H. pubinervia* (for which we have no pollinator observations). The long-tubed flowers of the rare *H. pubinervia* have an unusually narrow tube (Goldblatt, 2003), which may not accommodate the proboscis of a long-proboscid fly.

Flowers of most species in the *Hesperantha latifolia* group are visited and pollinated exclusively by long-proboscid flies in the family Nemestrinidae. In the southern African winter-rainfall zone, the long-tubed *H. latifolia* is pollinated by the nemestrinid *Prosoeca peringueyi,* while *H. oligantha* and *H. purpurea* are inferred to be pollinated by a second and undescribed *Prosoeca* species, *P.* sp. nov. (see Goldblatt et al., 1995; Manning & Goldblatt, 1996). Long-tubed species of the summer-rainfall zone, including *H. grandiflora, H. scopulosa,* and *H. woodii,* are pollinated by *P. ganglbauri,* while *H. brevicaulis* and *H. huttonii* are pollinated by *Stenobasipteron wiedemannii.* The elongated probosces of these flies are typically slightly shorter than the length of the perianth tubes of the *Hesperantha* species that they visit (Table 5), but these

flies are the only insects that are able to forage on the nectar held in the lower part of the perianth tube. While flowers of *H. stenosiphon* seem obviously adapted for long-proboscid fly pollination, we found no flies at our study site; instead, honeybees were visiting the flowers and collecting pollen. In doing so they were seen transporting pollen from anthers of one plant to style branches of another, effecting pollination.

An important exception in the *Hesperantha latifolia* group is the red-flowered form of the riverine species *H. coccinea* (Fig. 2D). This plant has two color morphs, the more common red-flowered form pollinated by a guild of large butterflies including *Aeropetes tulbaghia* (Satyridae) and *Papilio* species (Papilionidae). Visits by *Aeropetes* have also been reported by Johnson and Bond (1994). Johnson (pers. comm.) has also seen an unidentified long-proboscid fly visiting the red-flowered form, but this has been witnessed only once to date. The second color form of *H. coccinea* has a pink perianth. We have no observations on visitors to the pink form. Its pink perianth may indicate a dependence on long proboscid flies for pollination. Because only one color form of one species of *Hesperantha* is pollinated by large butterflies, it seems unreasonable to recognize an additional pollination group in the genus.

Flies grasp the tepals with their tarsi and probe for nectar while continuing to vibrate their wings, contacting anthers and stigmas with the ventral or lateral parts of the head and thorax. In the case of *Hesperantha grandiflora*, pollen deposition is always on the ventral part of the thorax because the unilateral stamens are positioned below the mouth

of the floral tube. Field observations and pollen load analyses show that all fly species visit open flowers of other species during foraging bouts and that most of these species have morphologically convergent flowers that may be regarded as belonging to specific pollination guilds. Thus, *Prosoeca peringueyi* visits a range of plants with intense red or violet flowers, including *Pelargonium magenteum* J. J. A. van der Walt (Geraniaceae) and species of Iridaceae such as *Babiana curviscapa* G. J. Lewis, *B. dregei* Baker, and *Lapeirousia silenoides* (Jacq.) Ker Gawl. (Manning & Goldblatt, 1996), as well as *H. latifolia* in the Kamiesberg of Namaqualand. Likewise, *Prosoeca ganglbauri* visits several pink-flowered species including *Gladiolus microcarpus* G. J. Lewis (Iridaceae), *Nerine bowdenii* S. Watson (Amaryllidaceae), and *Zaluzianskya microsiphon* (Kuntze) K. Schum. (Scrophulariaceae) during foraging bouts on *H. grandiflora* or *H. scopulosa* in the northern Drakensberg.

The Western Cape *Hesperantha pallescens* is exceptional in having pale yellow flowers with an elongate perianth tube with the flowers opening soon after sunrise and closing before sunset. The flowers conform to the model for species pollinated by another long-proboscid fly, *Philoliche* (Tabanidae) (Goldblatt et al., 1995; Goldblatt & Manning, 2000). To date we have not located a study population at an undisturbed site where the predicted pollinator is active, and we have seen no insect visitors to the species at our study site during apparently ideal conditions for insect activity.

Two patterns of butterfly behavior can result in pollen dispersal and pollen deposition. The first has been described as "inspection visitation" by Johnson and Bond (1994). A butterfly making an inspection visit does not land or feed on a flower, but its comparatively long body and broad wings often brush against the anthers and long style branches or stigmas as it swoops close to an open flower before moving to another, sometimes of the same species. In contrast, a true foraging visit requires that the butterfly actually grasp the tepals and insert its proboscis into the floral tube. In doing so, the ventral surface of the thorax and proximal abdomen become dusted with pollen. Butterflies noted and captured visiting red-flowered *Hesperantha coccinea* include *Papilio demodocus*, *P. nereis*, and *Aeropetes tulbaghia*, the latter also reported by Johnson and Bond (1994) to be a pollinator of this plant.

The Hesperantha vaginata *Group*

The *Hesperantha vaginata* group (Table 2) includes only *H. vaginata* and *H. karooica* Goldblatt

(not studied), which have unscented, bright yellow flowers, often marked with bold splashes of contrasting dark brown color (Fig. 2E). These flowers have a relatively short tube, 5–8 mm long, that produces no measurable nectar. The tepals, 30–35 mm long, much exceed the length of the tube. These flowers open during the middle part of the day, 13:00 H in *H. vaginata,* and close in the late afternoon, ca. 18:00 H in warm weather.

Hesperantha vaginata is visited exclusively by the hopliine beetle *Clania glenlyonensis* (identified as *Lepisia* sp. 1 in Goldblatt et al., 1998b) (Table 6). The flowers have the stereotyped adaptations for the hopliine beetle pollination system, a large flower with spreading or somewhat cupped tepals, reduced perianth tube, absence of nectar, and bold contrasting pigmentation (so-called beetle marks) (Picker & Midgley, 1996; Goldblatt et al., 1998b; Steiner, 1998). *Clania* individuals spend a considerable time in a flower, either crawling about or at rest with their heads pointed toward the center for up to 20 minutes. Sometimes their visits may last much longer, and beetles may even spend the night in the closed flowers. Hopliine beetles use the flowers of *H. vaginata* and some other species growing nearby, including *Romulea monadelpha* (Sweet) Baker (Iridaceae) and *Arctotis acaulis* L. (Asteraceae), as sites for assembly, intraspecific competition, and mating. They are invariably covered with a combination of pollen of *H. vaginata* and the co-blooming species listed above. Although these beetles feed on pollen and sometimes on tepal tissue, they do little or no damage to flowers (Steiner, 1998; Goldblatt et al., 1998b).

DISCUSSION

Pollination biology varies among *Hesperantha* species but correlates closely with the mode of floral presentation, timing of anthesis, and nectar secretion. Contrary to past predictions (Scott Elliot, 1891; Marloth, 1915; Vogel, 1954), white-flowered species that have flowers opening in the late afternoon and remaining open at night are not exclusively pollinated by moths. Indeed, our studies of the floral biology of *Hesperantha,* incomplete as they are, highlight the danger of inferring the pollination systems of plants with limited fieldwork or entirely from floral morphology. Marloth (1915: plate 42) suggested the genus was primarily pollinated by moths, based on his observation of small moths (not identified) seen visiting *H. falcata.* Vogel (1954) carried this further in suggesting that long-tubed species including *H. flava, H. grandiflora, H. longituba* (by which he probably meant *H. huttonii*),

and *H. pulchra* were pollinated by sphinx moths. The last three species have odorless, pink flowers that close at night. Vogel also speculated that the yellow and brown, short-tubed flowers of *H. vaginata* (which he knew as *H. metelerkampiae*) and the pink-flowered *H. pauciflora* were pollinated by bees (Vogel, 1954: 103). He was partly correct only in his assessment of *H. pauciflora,* and possibly of *H. flava,* for which we await field observations.

At first glance the adaptive radiation of pollination systems in *Hesperantha* parallels that found in larger genera of the Iridaceae in southern Africa, but with an unusual emphasis on white flowers opening in the late afternoon or evening, a pattern best developed in the southern African winter-rainfall zone. Specifically, Bernhardt and Goldblatt (2000) noted the number of pollination systems in an African genus of the Iridaceae correlates positively with the number of species in the genus. Genera containing more than 100 species (e.g., *Gladiolus* and *Moraea*) have the most diverse pollination systems exploiting up to eight broad categories of pollen vectors. With the exception of *Ferraria* (ca. 12 species) and *Sparaxis* (15 species), genera of Iridaceae with less than 20 species (e.g., *Micranthus, Nivenia*) do not have more than two modes of animal pollination (Goldblatt et al., 2000a; Bernhardt & Goldblatt, 2000; unpublished data). *Hesperantha,* with 79 species, *Geissorhiza* (85 spp.), *Ixia* (ca. 50 spp.), and *Lapeirousia* (40 spp.) each have four or five major pollination modes (Goldblatt et al., 1995, 2000b; Bernhardt & Goldblatt, 2000).

Four major modes of pollination (bee and crepuscular settling moth; diurnal bee; hopliine beetle; long-proboscid fly, or large butterfly) are confirmed for *Hesperantha* based on our field observations and collection of floral foragers with analysis of their pollen loads. A fifth mode of pollination by sphingid moths, predicted by Vogel (1954) for *H. flava,* remains to be confirmed by future field investigation.

Furthermore, pollination systems in *Hesperantha* also subdivide along predictable modes of floral presentation already described in other genera of Iridaceae. This is most striking in the *H. latifolia* group where tubular, odorless flowers with different patterns of floral pigmentation are pollinated by different genera or species of two families of long-proboscid flies. As described in the genera *Babiana, Gladiolus,* and *Lapeirousia,* tubular flowers that are pink to the human eye (e.g., *H. brevicaulis, H. grandiflora, H. huttonii, H. woodii*) are most likely to be pollinated by the Nemestrinidae *Prosoeca ganglbauri* and *Stenobasipteron wiedemannii.*

In contrast, those with intense blue to purple flowers (e.g., *H. latifolia, H. oligantha*) are pollinated by *Prosoeca peringueyi* or an undescribed *Prosoea* species. Pale yellow to cream, tubular flowers are more likely to be pollinated by long-proboscid tabanids in the genus *Philoliche* (Goldblatt et al., 1995; Goldblatt & Manning, 2000; Manning & Goldblatt, 1996, 1997).

UNIQUE TRENDS IN THE FLORAL ECOLOGY OF
HESPERANTHA

Pollination systems incorporating large-bodied bees, long-proboscid flies, or hopliine scarab beetles have been well described in 14 other genera of the Iridaceae of southern Africa and are not in any manner unusual in *Hesperantha* (Bernhardt & Goldblatt, 2000). There are, however, two modes of pollination in this genus atypical of the family. First, pollination by deceit is suggested in the tubular, pink flowers of *H. pubinervia* and *H. scopulosa.* While both species have the pigmentation and floral tube length of nectariferous species pollinated by long-proboscid flies, both fail to secrete nectar. As this mode of floral presentation is virtually identical in co-blooming species pollinated by the same flies, *H. pubinervia* and *H. scopulosa* evidently represent either Batesian or guild mimics. These two modes of deceit are more common in the Orchidaceae (Dafni & Bernhardt, 1989), including the southern African genus *Disa* (Johnson, 1994; Johnson et al., 1998). Second, our documentation of pollination mechanisms in the *Hesperantha falcata* group is the first record in the Iridaceae of species either exploiting both settling moths of five lepidopteran families with crepuscular to nocturnal foraging habits and large-bodied apid bees (*Anthophora* and *Apis*), or settling moths alone. While generalist pollination systems combining bees and Lepidoptera have been described in a few species of *Lapeirousia* (Goldblatt et al., 1995), these species depend on true butterflies and sometimes moths with diurnal habits. In contrast, full floral presentation by species of the *H. falcata* group begins at twilight. Thus, while several species of the *H. falcata* group attract large-bodied bees, *Gladiolus* and *Lapeirousia* species receive the majority of their visits from bee pollinators from mid morning to early afternoon, and their flowers often close at night. Bee pollination in the *H. falcata* group only begins at the end of the day, and flowers remain open after sunset to exploit a second group of pollinators that belong to another order of insects.

Other genera of the African Iridaceae in which moth pollination is known or inferred, *Babiana* (un-

published data), *Gladiolus* (Goldblatt et al., 2001; Goldblatt & Manning, 2002), and *Lapeirousia* (Goldblatt et al., 1995), have larger flowers with a relatively long perianth tube, and are visited either by hovering sphinx or noctuid moths with long probosces. The foraging pattern in these species is unlike that shown by small moths on *Hesperantha* flowers, in which individuals crawl over the inflorescence, visiting one flower after another before moving to another plant.

The dark red or brown pigmentation on the reverse of the outer tepals of most otherwise white-flowered species of the *Hesperantha falcata* group may be a form of crypsis. When the perianth is closed, only the outside of the outer tepals is visible, and the dark color presumably camouflages the perianth from both herbivorous beetles and nectar-robbing bees. Johnson (1995) postulated a similar reason for the dark red color of the orchid *Disa* (*Monadenia*) *ophyridea* (Lindl.) Bolus, which is also pollinated by noctuid moths. These flowers cannot close fully, hence the heightened need for cryptic coloration to prevent nectar and pollen robbers. In this species moths evidently locate flowers solely by olfactory cues.

At first glance, butterfly pollination in *Hesperantha coccinea* appears to converge with the *Aeropetes tulbaghia* pollination system described by Johnson and Bond (1994). These authors have described a true guild of red-flowered species that bloom primarily in the southern African winter-rainfall zone and are pollinated almost exclusively by the large satyrid butterfly *A. tulbaghia*. This guild includes several species in the Amaryllidaceae and Iridaceae and is characterized by the large, bright red flowers, sometimes with white nectar guides, relatively narrow floral tubes and ample, but relatively dilute nectar. Although it occurs in the southern African summer-rainfall zone, *Hesperantha coccinea* appears to fit this profile, but more important, it is not pollinated exclusively by *Aeropetes*, unlike the guild of large butterfly flowers in the winter-rainfall zone. The pollination system of *H. coccinea* also incorporates some of the larger species of butterflies in the family Papilionidae. Thus even though *Aeropetes* has a strong, innate attraction for red flowers, it is not the only visitor to red butterfly flowers in southern Africa. The lack of pollination by other large butterflies in the winter-rainfall zone may simply reflect the seasonal scarcity of other large butterflies there. We note that other large butterfly flowers of the summer-rainfall zone include red-flowered species such as *Bauhinia galpinii* N. E. Br. (Fabaceae), *Gloriosa superba* L. (Colchicaceae), as well as those of other colors

such as blue-flowered *Plumbago auriculata* Lam. (Plumbaginaceae). In eastern southern Africa *Aeropetes* seems to have a weaker affinity for red flowers and often visits yellow flowers of *Kniphofia* (Asphodelaceae), in addition to the red flowers of plants such as *Gladiolus saundersii* J. D. Hook. (Goldblatt & Manning, 2000, 2002) as well as *H. coccinea*. It is unlikely that red pigmentation and tubular flowers limit the access of large butterflies other than *A. tulbaghia* in the classic definition of butterfly pollination (Faegri & van der Pijl, 1979), in which red pigmentation and a narrow floral tube are relatively common.

POLLINATION SHIFTS IN *HESPERANTHA*

With the exception of species of the *Hesperantha falcata* group, pollination systems in this genus reflect the exploitation of the usual range of southern African insects responsible for pollination in the family. In contrast to other genera of Iridaceae, however, we also note that minimal shifts in floral characters are all that has been required to change a pollination system.

In particular, the morphological modification of *Hesperantha* flowers has been limited to the length of the perianth tube and the orientation of the tepals at anthesis. This conservative trend must be compared to the shifts in the pollinations systems of *Moraea* requiring severe changes in tepal orientation and differentiation of the inner and outer tepals and in the morphology of the staminal column and style branches (Goldblatt & Bernhardt, 1999). We must also compare the relatively conservative perianth morphology of *Hesperantha* with that of *Gladiolus* in which floral symmetry and floral tube shape and orientation change with the primary pollinators (Goldblatt & Manning, 1998; Goldblatt et al., 1998a). Instead, significant alterations of floral presentation in *Hesperantha* are limited to relatively minor shifts in floral pigmentation, correlated with variation in scent production and nectar secretion. Indeed, to the human eye *Hesperantha* flowers appear to lack the unusually complex, contrasting patterning of pigmentation typical of the flowers of most other genera of the family in southern Africa.

Comparatively minor differences in nectar sugar composition and concentration have had a dramatic effect on which insects are most likely to pollinate a *Hesperantha* flower, for the important reason that these biochemical characters evolved in association with shifts in the mechanics of floral phenology. Specifically, the stereotyped opening and closing of tepals in different species, at different seasons, and

at different times of the same day sharply restricts foraging by prospective pollinators. Mature flowers that remain closed while particular species of anthophilous insects are actively searching for edible rewards are almost as effectively excluded from developing novel interactions as they would be if they bloomed at a time of the year when the same insects are absent.

A change in pollinator from an insect with relatively short mouth parts, such as apid bees, short-proboscid nemestrinids, small moths, and possibly other polyphagic taxa, to one with longer mouth parts, such as long-proboscid nemestrinids, may seem a relatively moderate shift and merely one of degree. It must, however, be remembered that a shift to a long-proboscid fly pollinator means a change from a system where several species of bee and fly, or several different species of moth, may pollinate a species to one where only a single species is the primary or sole pollinator. Long-proboscid flies are particularly effective pollinators of certain plants because relatively few plants offer them a reliable source of nectar, and they usually carry heavy loads of pollen on specific parts of their bodies, limiting or avoiding stigma clogging (Goldblatt & Manning, 2000). The shorter-tongued insects, however, visit many species, sometimes in a nonconstant pattern, and they usually carry mixed loads of pollen that are often randomly scattered over their bodies. These contrasting patterns of pollination must have important consequences for the reproductive systems of the two plant groups. A shift to a specialist pollination system using just one pollinator species presumably has important consequences for the radiation of a genus despite the apparently trivial shift in morphology and physiology.

DISTRIBUTION OF POLLINATION SYSTEMS

In the absence of any phylogenetic hypotheses about the radiation of *Hesperantha*, the origin and evolution of pollination systems in the genus remains a speculative topic. Small white, crepuscular or nocturnal flowers are unknown in subfamily Crocoideae outside the genus, and this pollination system must be derived. Flowers in *Geissorhiza*, the genus to which *Hesperantha* is most closely related (Lewis, 1954; Goldblatt, 1984; Reeves et al., 2001), may be pink, blue, violet, or white, but are always diurnal. The most common, and presumably ancestral pollination system in *Geissorhiza* is a generalized one (Nänni, unpublished data) in which the small, short-tubed flowers are open during the day and offer both pollen and small quantities of nectar.

They are visited by a range of insects including *Apis mellifera*, hopliine beetles, butterflies, bee flies (Bombyliidae), and short-proboscid tabanid and nemestrinid flies, and these species may be considered generalists. The pollination system in *Hesperantha* that most closely resembles this system is the large-bodied *Apis mellifera*–anthophorine bee, hopliine beetle, and short-proboscid nemestrinid fly system found in the winter-rainfall zone *H. pauciflora*, and the anthophorine bee system in such eastern southern African species as *H. baurii, H. lactea,* and *H. similis.*

The long-proboscid fly pollination system in *Hesperantha* is, we assume, derived, since it is a more specialized system than those using a wider range of pollinators. The taxonomic distribution of the strategy in the genus makes it clear that it has had multiple origins (Goldblatt, 2003). The eastern southern African species pollinated by *Prosoeca ganglbauri* or *Stenobasipteron wiedemannii* may share a common ancestry. However, the Namaqualand *H. latifolia*, pollinated by *Prosoeca peringueyi*, and the western Karoo *H. oligantha*, inferred to be pollinated by an undescribed *Prosoeca* species, belong to different taxonomic sections of *Hesperantha* (according to Goldblatt, 1984, 2003). Long-proboscid fly pollination is also inferred for two apparently unrelated species of *Hesperantha* sect. *Radiata*, the eastern Cedarberg *H. elsiae* and the southern Cape *H. muirii*, based on flowers with an elongate perianth tube and pink coloration. These two species are most likely local derivatives of the widespread *H. radiata*, the nocturnal flowers of which are pollinated by moths. Thus, while we can say little about the origins of moth pollination in *Hesperantha* flowers, it is clear that long-proboscid fly pollination evolved several times in the genus and involves different species of nemestrinid (and possibly tabanid) flies across the range of the genus in southern Africa. This mirrors the pattern in *Gladiolus* (also belonging to the Crocoideae), in which long-proboscid fly pollination may have evolved at least 10 and possibly 12 times in this genus of 165 species in southern Africa (Goldblatt & Manning, 1999; Goldblatt et al., 2001).

The shift to butterfly pollination in red-flowered populations of *Hesperantha coccinea* is unique in the genus. Although butterflies may share this riverine species with long-proboscid flies, it seems likely that only the rare pink-flowered populations, which Occam's razor suggests must be ancestral, are normally pollinated by long-proboscid flies. The red-flowered populations, which extend from the Amatola Mountains in Eastern Cape Province, South Africa, to Zimbabwe, are pollinated largely,

if not exclusively, by a range of large butterflies, including species of Papilionidae and the satyrid *Aeropetes.*

The shift to exclusive hopliine beetle pollination in *Hesperantha vaginata* (and perhaps its close ally *H. karooica*) is likewise unique in the genus, but flowers shared by apid and anthophorine bees and hopliines occur in a few other species of *Hesperantha,* notably *H. pauciflora.* The evolution of a strictly hopliine pollination system is thus not particularly surprising.

In summary, the radiation of pollination systems in *Hesperantha,* a mid-sized genus of subfamily Crocoideae of the Iridaceae, is not unexpected in view of the diversity of pollination systems in most other genera of any size in the subfamily. Each genus, however, appears to exploit the available spectrum of pollinators in different ways and to different degrees. *Ixia* exhibits a remarkable pattern of radiation based on hopliine beetle pollination and secondarily on long-proboscid flies, whereas *Gladiolus* exploits in particular anthophorine bee pollination, with secondary emphasis on long-proboscid flies, Lepidoptera, or passerine birds. *Lapeirousia* has exploited a range of different long-proboscid flies as pollinators, while a few species have flowers adapted for sphinx or other moth pollination, but some species are pollinated by a combination of bees, wasps, and butterflies.

The pattern of radiation in *Hesperantha* shows particularly marked exploitation of long-proboscid fly pollination in eastern southern Africa, where 11 of the 34 species there (Goldblatt, 2003) have flowers that display the typical adaptations for this strategy. In contrast, species of the southern Africa winter-rainfall zone have exploited small moth pollination (or a combination of moths and apid and anthophorine bees) at the expense of most other pollination systems. Hopliine beetle, exclusive anthophorine bee, and long-proboscid fly systems are limited to only a few species there. Some 22 of the 44 species in the winter-rainfall zone have been shown herein, or may confidently be inferred, to have this small settling moth pollination system, often associated with foraging by large anthophorine bees late in the day, a system not otherwise known in the Iridaceae.

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Figure 3. The principal flower types in Hesperantha. A. H. pauciflora (typical bee flower with relatively short perianth tube, pink color, and open in the day). B. H. cucullata (typical settling moth flower with relatively short perianth tube, white color with reddish pigment on outside of outer tepals, opening near sunset and lasting into the night). C. H. woodii (long-proboscid fly flower with elongate perianth tube, pink perianth, open during the day). D. H. vaginata (beetle flower with vestigial tube, cupped perianth, brightly colored with contrasting markings, open in middle of the day) with hopliine beetle Clania glenlyonensis in the flower.