
Volume 85
Number 2
1998

Annals
of the
Missouri
Botanical
Garden



POLLINATION OF PETALOID
GEOPHYTES BY MONKEY
BEETLES (SCARABAEIDAE:
RUTELINAE: HOPLIINI) IN
SOUTHERN AFRICA¹

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ABSTRACT

Field observations, floral dissections, and pollen load analyses of insects indicate that pollination by hopliine beetles (Scarabaeidae: Rutelinae: Hopliini) has evolved convergently in many genera of herbaceous perennials in southern Africa. Beetle-pollinated flowers are identified by a suite of characters including a salver- to shallow bowl-shaped perianth and pigmentation emphasizing bright colors (red, orange, cream). Stereotyped "beetle marks" of either pale or dark color are frequently present at the bases of tepals or petals. These flowers are typically odorless and rarely offer nectar. Beetles, however, consume anthers and pollen, which are often a contrasting color from the perianth. Taxa that are pollinated by hopliine beetles include species in genera of the Hyacinthaceae (*Daubenia*, *Ornithogalum*), Iridaceae (*Aristea*, *Homeria*, *Ixia*, *Moraea*, *Romulea*, *Sparaxis*, *Tritonia*), and Hypoxidaceae (*Spiloxene*) in the monocots and Asteraceae (*Arctotis*, *Ursinia*), Campanulaceae (*Prismatocarpus*, *Wahlenbergia*), and Droseraceae (*Drosera*) among the dicots. Hopliine pollinators include both male and female beetles in the genera *Anisonyx*, *Anisochelus*, *Heterochelis*, *Khoina*, *Lepisia*, *Lepithrix*, *Pachycnema*, and *Peritrichia*. These beetles visit flowers to consume pollen and possibly nectar, to compete for mates, and to copulate. Pollen is usually deposited on or between hairs on the exoskeleton. The suite of characters associated with beetle pollination in these herbaceous geophytes is closer to that described in the herbaceous perennials of the eastern Mediterranean Basin and the woody flora of eastern Australia than it is to the classic series of features associated with magnoliid angiosperms.

The consumption of floral rewards (e.g., pollen, nectar, starchy food bodies, epidermal tissue) by Coleoptera has been well documented, and the mechanics of consumption and digestion of pollen, in particular, are extremely variable in beetles. Most beetles studied have either a pollen-cracking "molar" on their mouth parts or swallow pollen grains

whole in the presence of hydrating nectar. In a few cases beetles may consume hard trichomes with pollen and use these plant cells as a pollen cracking grit (see review in Bernhardt, 1996). Knowledge of the role of beetles as pollinators of angiosperms has, however, changed radically in the last 15 years. In the classical view of beetle pollination,

¹ Support for this study by grants 4816-92 and 5408-95 from the National Geographic Society is gratefully acknowledged. We thank Holger Dombrow, Worms, Germany, and M. J. Picker, University of Cape Town, for their help with identifications of hopliine beetles.

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reviewed by Faegri and van der Pijl (1979), beetles were associated primarily with the pollination of basal angiosperms, especially magnoliids, Araceae, and Cyclanthaceae (Armstrong, 1979; Bernhardt & Thien, 1987). Beetle pollination is traditionally associated with chamber- or urn-like flowers or inflorescences, absence of bright coloration, strong, unpleasant odors, and anthers that often extrude their pollen upon dehiscence. "Beetle flowers" shelter their pollinators, e.g., *Stapfia* (Gottsberger, 1977), but are not usually associated with true nectar secretion. The major pollinators of such flowers are comparatively small nitidulid, curculionid, and staphylinid beetles. Large-bodied dynastine scarab beetles have been associated with the pollination of *Victoria* (Prance & Arias, 1975), *Cyclanthus* (Beach, 1982), and a number of species of Araceae (Gottsberger & Amaral, 1984) and Annonaceae (Gottsberger, 1989a, 1989b).

This view of beetle pollination has expanded radically with ongoing research in temperate-tropical Australia and in the eastern Mediterranean. Work in Australia (Hawkeswood, 1987) showed that large brightly colored buprestids, cerambycids, and scarabs consumed the nectar in bowl-shaped flowers of the Myrtaceae and Burseraceae. Unlike the magnoliids and palms, these plants have flowers with anthers elevated on long stiff filaments, and the beetles often reach the nectar by pushing the filaments aside or crawling between them (Hawkeswood, 1987; photograph by Hawkeswood in Bernhardt, 1993). To the human eye, these flowers are usually white or light pastel shades, and strong fruit-like odors suggesting fermentation are not detectable. In Israel, fieldwork and experimentation (Dafni et al., 1990) have shown that flowers with bowl-shaped, red to orange perianths, blackened tepal bases and/or pollen, and no discernible scent are pollinated almost exclusively by vernal scarabs in the genus *Amphicoma*. These insects are far hairier than the majority of beetles associated with the classic syndrome of cantharophily. Plants with flowers showing this suite of characters comprise a guild of herbaceous perennials dominated by Ranunculaceae and some petaloid monocots (Dafni et al., 1990).

Early work by Scott Elliot (1891) appears to contain the first reference to the importance of hopliine beetles in the pollination of the South African flora. Peringuey (1902) also remarked on the frequency of beetle pollination in southern African plants, noted floral foraging in many genera of native beetles, and suggested that their membranous mouth parts implied a diet emphasizing nectar. Peringuey noted that such beetles departed from flowers cov-

ered with pollen, and that "on a bright day in the spring (August–October) no flower is without a tenant." He maintained that few insects were better adapted for flower pollination than such genera of hairy beetles as *Anisonyx*, *Lepithrix*, and *Peritrichia*. Curiously, Vogel (1954) did not cite Peringuey in his mammoth review of pollination systems in southern Africa. Vogel did note that some scarab genera were pollen- and flower-eaters but made few overt references to beetle pollination, and the subject remained virtually dormant for the next 40 years. In their review of insect pollination systems in the Cape Flora (the winter-rainfall climate zone of southern Africa), Whitehead et al. (1987) derived most of their references to scarab pollination from Vogel (1954), although they did note that cetoniids, nitidulids, and staphylinids visited the flowers of some shrubby Proteaceae.

Recent evidence, however, now strongly suggests that scarab beetles in the subtribe Hopliini (tribe Rutelinae) comprise an important pollinator guild in southern Africa and that a suite of floral characters is associated with "monkey-beetle" pollination. Among the few works available to date on the pollination of southern African plants by the Hopliini is that of Picker and Midgley (1996), who listed some 25 species of plants as putatively monkey-beetle pollinated. These included both monocots and dicots representing some 10 families. More importantly, Picker and Midgley recognized three systems of monkey-beetle pollination, based on differences in beetle hairiness, flower color preferences, and whether foraging was restricted to pollen. Goldblatt and Manning (1996) described the foraging behavior of hopliine beetles in the genera *Anisonyx* and *Peritrichia* (as *Lepithrix*), concluding that they were most likely to be the dominant (or sole) pollinators of two species of *Drosera* (Droseraceae), and one species each of *Aristea* and *Moraea* (Iridaceae). These authors also suggested that other species of monkey beetles were likely to be the pollinators of many more species of Iridaceae in genera such as *Aristea*, *Homeria*, *Moraea*, *Romulea*, *Sparaxis*, and *Tritonia*. Studies by Steiner (1998 and pers. comm.) also show the importance of monkey-beetle pollination in the so-called peacock moraeas, *M. villosa* and its close allies, as well as in *Sparaxis* and genera of Asteraceae including *Arcototis*.

Obviously, additional fieldwork on beetle pollination in southern Africa is required. The problem is that while we have a number of observations of monkey beetles visiting flowers, there remains a paucity of data showing that these beetles transport pollen of their host flowers and actually contact

stigmatic surfaces. As Hawkeswood (1989) has shown, scarab beetles may pollinate the flowers of some species while destroying those of other co-blooming species. For example, while *Diphucephala affinis* (Scarabaeidae: Melolonthinae) regularly visits flowers of *Hibbertia* (Dilleniaceae) in western Australia, these scarabs fail to transport *Hibbertia* pollen or contact the stigmas. Here, we present our own observations on pollen foraging by beetles on native southern African geophytes and compare beetle pollination in southern Africa to that elsewhere in the world.

MATERIALS AND METHODS

Fieldwork was conducted during August to October 1995, and during the same months in 1996 and 1997 at several sites (Table 1) in the southwestern Cape (Cape Floristic Province) and the western Karoo, South Africa, areas of Mediterranean climate with wet winters and dry summers. Observations of insect foraging involved 4–20 hours per plant species, and included recording of floral attractants (pigment patterns, scent), the behavior of insects on the flower, and the taxonomic identity of floral foragers. Insects were not collected unless they were observed to contact the sexual organs of flowers while foraging or mating. Insects were captured and killed with ethyl acetate fumes for subsequent identification and analysis of pollen loads. To prevent contamination of one insect with pollen carried by another in the same killing jar, individuals were isolated by wrapping in tissue paper.

Removal of pollen from insect bodies involved either gently scraping pollen off the body with a dissecting needle or gently washing the insect bodies in drops of 95% ethanol. The residue from needle probes or washes was collected on glass slides and mounted in 1–2 drops of Calberla's fluid (Ogden et al., 1974). The pollen of a particular plant species was scored as present on the body of an insect if more than 10 individual grains (or polyads) were counted on the slide (Tables 3, 4). Pollen grains were identified by comparison with a reference set of pollen-grain preparations made from plants flowering at our study sites.

Field determinations of nectar (if present) were made by withdrawing nectar from the base of the floral tube with 2 μ l capillary tubes after separating the ovary from the perianth. Nectar samples were dried on filter paper and sent to B.-E. van Wyk, Rand Afrikaans University, Johannesburg, for HPLC analysis. The percentage of sugars dissolved in fresh nectar was recorded on a Bellingham &

Stanley hand-held refractometer (0–50%) using nectar extracted from flowers in the manner described above. When volumes were too small to measure or to determine sugar concentration, presence of nectar was established by brushing nectariferous areas of flowers against the tongue.

Identifications of beetles were made by M. Picker, University of Cape Town, and H. Dombrow, Worms, Germany. Flies were determined by J. C. Manning and bees by Robert Brooks, Snow Entomological Museum, University of Kansas. Voucher specimens were made of plant species visited by beetles when necessary; these specimens are deposited at MO and NBG (Table 2). Insect vouchers are deposited at the Snow Entomological Museum and/or the South African Museum.

RESULTS

FLORAL PHENOLOGY AND HABIT

Flowers visited most often by hopliine beetles (monkey beetles) are largely restricted to the winter-rainfall region of southern Africa, namely the southern and western coast of the subcontinent and the near interior. Flowering there is concentrated in the late winter and late spring, August to early November (Table 2). The majority of flowers observed to be visited by beetles belong to herbaceous perennials, especially geophytic petaloid monocots, and subshrubs (Aizoaceae subfam. Mesembryanthemoideae, some Asteraceae).

These species typically form fairly dense populations locally, with over 10 individuals per square meter not uncommon. In some species, e.g., *Gladolus meliusculus* and *Ixia polystachya*, plants tend to be much more scattered, typically of the order of 1–2 m apart.

FLORAL PRESENTATION AND REWARDS

The majority of flowers visited by monkey beetles have salver- to shallow bowl-shaped, actinomorphic perianths or involucrel inflorescences (Asteraceae). Species of Iridaceae subfamily Ixioidae studied (Table 2) have a short, cylindric or more or less funnel-shaped perianth tube, 1.5–10 (rarely to 20) mm long. In species of *Ixia* sect. *Ixia* (*I. curta*, *I. dubia*, *I. maculata*, *I. cf. polystachya*), *Romulea*, *Sparaxis*, and *Tritonia* the tube is filiform below and blocked by the style, and sometimes the mouth of the tube is closed off by the fused or coherent filaments. These nectarless tubes appear to be inaccessible to the mouth parts of the foraging insects described below.

Floral colors are extremely variable (Table 2), but

Table 1. Plant species pollinated or visited by hopliine beetles and study sites. Dates of observation are included in column 3. Parentheses in column 1 indicate species apparently visited casually by hopliine beetles and in column 2 insect species other than hopliine beetles. Their orders and families are as follows: Apoidea: *Andrena* (Andrenidae), *Apis mellifera* (Apidae), halictid bees (Halictidae); Muscoidea: *Philoliche* (Tabanidae); *Musca*, *Orthellia* (Muscidae); *Scathophaga* (Sarcophagidae); *Anthomyia* (Anthomyidae).

Plant species	Hopliine beetles (other insects)	Study site (date of observation)
<i>Homeria ochroleuca</i>	<i>Anisonyx ursus</i> , (<i>Apis mellifera</i> , <i>Scathophaga stercoraria</i> , <i>Orthellia</i> sp., <i>Anthomyia</i> , Calliphoridae, Syrphidae)	Sir Lowry's Pass Village (Aug. 1995)
<i>Babiana rubrocyanea</i> , <i>Gladolus meliusculus</i> , <i>Ixia maculata</i> , <i>Romulea eximia</i> , <i>R. obscura</i> , <i>Spiloxene capensis</i>	<i>Lepisia rupicola</i> , <i>Pachynema crassipes</i> , (<i>Andrena</i> sp.)	Waylands Reserve, Darling (Sep. 1995, 1996)
<i>Ixia framesii</i> , <i>Arctotis acaulis</i> , <i>Ornithogalum thyrsiflora</i>	<i>Lepithrix ornatella</i> , (<i>Philoliche atricornis</i>)	Camphill road, Malmesbury (Sep. 1995)
<i>Ixia maculata</i> , <i>Ornithogalum thyrsiflora</i>	<i>Pachynema crassipes</i> , <i>Lepithrix longitarsis</i> , <i>L. fulvipes</i>	Ysterfontein, Clanwilliam (Sep. 1995)
<i>Ixia maculata</i> , <i>Ornithogalum thyrsiflora</i>	<i>Pachynema crassipes</i> , <i>Heterochelis arthriticus</i> , <i>Scelophysa militaris</i> , <i>Lepithrix ornatella</i>	Sandberg, Leipoldtville (Sep. 1995)
<i>Ixia dubia</i> , <i>Moraea bellendenii</i>	<i>Heterochelis arthriticus</i> , <i>Pachynema crassipes</i> , <i>Lepithrix ornatella</i> , <i>Heterochelis unguicularis</i>	Darling, renosterveld (Sep. 1996)
<i>Ixia curta</i> , <i>Ursinia</i> sp., <i>Gazania krebiana</i> , <i>Monsonia speciosa</i>	<i>Pachynema crassipes</i> , <i>Lepisia rupicola</i>	Versveld Reserve, Darling (Sep. 1996)
<i>Tritonia crocata</i> , <i>Ornithogalum dubium</i>	<i>Pachynema tibialis</i>	Riversdale commonage (Sep. 1995)
<i>Tritonia deusta</i>	<i>Peritrichia hybrida</i>	Swellendam (Oct. 1997)
<i>Tritonia squalida</i> , <i>Agathosma</i> sp.	<i>Peritrichia</i> sp. 1	Blombos road, Riversdale (Oct. 1997)
<i>Homeria elegans</i> , <i>Aristea teretifolia</i> , <i>Hesperantha falcata</i>	<i>Peritrichia pseudoplebeia</i> , (<i>Apis mellifera</i> , <i>Orthellia</i> sp., <i>Scathophaga stercoraria</i>)	Fairfield Estate, Bredasdorp (Aug. 1995, Sep. 1996)
<i>Aristea lugens</i> , <i>Moraea villosa</i> , <i>Agathosma</i> sp., (<i>Geissorhiza aspera</i>)	<i>Anisonyx longipes</i> , <i>A. ursus</i> , <i>Lepithrix ornatella</i>	Malmesbury commonage (Sep. 1995, 1996)
<i>Aristea cantharophila</i> , <i>Moraea</i> cf. <i>lurida</i> , <i>Drosera</i> spp.	<i>Peritrichia pseudoplebeia</i> , <i>Anisonyx ursus</i> , (<i>Musca</i> sp.)	Sir Lowry's Pass (Aug.–Sep. 1995)
<i>Sparaxis elegans</i> , <i>Arctotis acaulis</i> , <i>Ursinia cakilefolia</i> (<i>Homeria bifida</i>)	<i>Lepisia</i> sp. 1, (<i>Philoliche atricornis</i>)	Bokkeveld Plateau, Glenlyon renosterveld (Sep. 1995, Oct. 1996)
<i>Sparaxis elegans</i> , <i>Ursinia cakilefolia</i>	<i>Anisochelus inornatus</i> , (<i>Philoliche atricornis</i>)	Nieuwoudtville church yard (Sep. 1997)
<i>Hesperantha vaginata</i> , <i>Romulea monadelpha</i> , <i>Sparaxis pillansii</i> , <i>Bulbinella elegans</i> , <i>Arctotis acaulis</i> , <i>Berkheya glabrata</i>	<i>Lepisia</i> sp. 1, (<i>Philoliche atricornis</i>)	Bokkeveld Escarpment, Glenlyon dolerite (Sep. 1995, 1966)
<i>Romulea monadelpha</i> , <i>Arctotis acaulis</i>	<i>Lepisia</i> sp. 1	Near Calvinia (Oct. 1996)
<i>Romulea sabulosa</i>	<i>Lepithrix stigma</i>	Bokkeveld Escarpment, Oorlogskloof road (Sep. 1996)
<i>Romulea sabulosa</i>	<i>Lepithrix stigma</i>	Bokkeveld Escarpment, Grasberg road (Sep. 1995)
<i>Homeria vallisbelli</i> , <i>Romulea montana</i> , <i>Spiloxene capensis</i> , (<i>Oxalis obtusa</i>)	<i>Anisochelus inornatus</i>	Bokkeveld Escarpment, Keyzerfontein road (Sep. 1996)
<i>Daubenya aurea</i> , <i>Romulea subfistulosa</i>	<i>Lepisia</i> sp. 2, (<i>Halictid</i> bees)	Roggeveld Escarpment (Sep. 1995)

Table 1. Continued.

Plant species	Hopliine beetles (other insects)	Study site (date of observation)
<i>Moraea insolens</i> , <i>Ixia flexuosa</i> , <i>Aristea biflora</i>	<i>Anisonyx lepidotus</i>	Drayton, Caledon (Oct. 1996)
<i>Aristea biflora</i> , <i>Drosera pauciflora</i> , <i>Spiloxene capensis</i>	<i>Anisonyx lepidotus</i>	Near Drayton, Caledon (Sep. 1997)
<i>Thereianthus racemosus</i>	<i>Khoina bilateralis</i>	Zuurvlakte, Grootwinterhoek (Nov. 1995)
<i>Ixia</i> cf. <i>polystachya</i> , <i>Ornithogalum dubium</i> , <i>Prismatocarpus pedunculatus</i>	<i>Peritrichia subsquamosa</i> , (<i>Pachyne- ma saga</i> —only <i>Prismatocarpus</i>)	Brandvlei hills, Worcester (Nov. 1996)
<i>Sparaxis grandiflora</i> , Asteraceae spp.	<i>Peritrichia rufotibialis</i> , <i>Anisocheilus inornatus</i> , (<i>Philoliche atricornis</i> , Halictid bees)	Citrusdal—Clanwilliam (Sep. 1997)

intense yellow, bright orange to red, or purple shades predominate at most sites. Contrasting pigmentation may be seen at two different levels. The majority of beetle-visited flowers have dark, or sometimes pale, marks on the tepals or petals (Figs. 1–6), sometimes superimposed on a calloused epidermis (Table 2). In petaloid geophytes, these markings may take the form of a central blotch encompassing the bases of all the tepals and sometimes the filaments (e.g., *Aristea cantharophila*, *Ixia maculata*), or one or both tepal whorls may have quite discrete marks composed of ovate areas of contrasting pigmentation, sometimes with hazy edges (e.g., *Aristea teretifolia*) or sometimes with a paler or darker central line that resembles the line between the elytra when at rest (Figs. 1, 4, 6). We provisionally call these markings “beetle marks” both for the frequent resemblance to the shape of a beetle and for the presumed function of attracting beetles to flowers. The color of the markings may be black (*Aristea lugens*), light to dark brown (*A. teretifolia*, *Ixia curta*, *I. maculata*), or greenish or even yellow on a darker background, and then most often with median dark lines. The markings on the tepals of dark red-flowered *Romulea eximia* and *R. obscura* are light green and closely resemble the beetle *Lepisia rupicola* often seen on their flowers (Goldblatt & Manning, 1996 with color photograph). The floral markings on *Aristea biflora* and *Tritonia crocata* subsp. *hyalina* consist of transparent oval areas at the lower edges of the tepals, which appear dark when viewed from above. The presence of beetle marks on flowers of *Babiana rubrocyanea* is questionable: the deep blue flowers have a uniform, large, bright red center rather than a discrete dark, beetle-like mark. The presence of beetle marks in the flowers of *Ixia dubia* varies from population to population. Flowers observed near Rondebeg have typical dark markings at the tepal bases, whereas these marks are absent in plants from near Darling.

The second level of contrasting pigmentation consists of anthers or pollen of unusual color. The anthers and pollen may be bright orange (Table 2) and thus prominent against dark-colored perianths or filaments, and sometimes the anthers may be black, then presumably forming part of the beetle marks (*I. monadelpha*, *I. cf. polystachya*). The anthers are sometimes unusually large, particularly so in *Homeria elegans* (8–10 mm) and some species of *Aristea* (4.5–7 mm) and *Ixia* (6–10 mm), compared with anthers in other species of these genera.

Floral fragrances were not noted in the majority of species. Flowers of *Homeria elegans* have a sweet odor reminiscent of shredded coconut, whereas those of *H. ochroleuca* have a mild, slightly acrid, musk-like odor reminiscent of flowers of *Rhus* spp. (Anacardiaceae). *Gladiolus meliusculus* has a strong, sweet, honeyed fragrance like that of *Viola odorata* (Goldblatt & Manning, 1998).

The majority of species studied have no discernible nectar glands, and floral nectar does not appear to be secreted. Trace amounts of nectar are present as a wet sheen toward the base of the floral tubes of *Ixia framesii* and species of *Romulea*, *Sparaxis*, and *Tritonia*. *Gladiolus meliusculus* secretes nectar at the base of the floral tube [0.8–1.2 μ l, 29.2% (SD:1.3) sucrose equivalents, sucrose dominant, n = 5], while *Homeria ochroleuca* secretes nectar on the lower surfaces of the tepals (0.2 μ l, concentration not measurable, equal quantities of fructose and glucose and no sucrose). Nectar and/or fragrance were evident only in those species that were visited by a combination of beetles and other insects.

BEETLE DIVERSITY AND PHYSICAL PARAMETERS

Coleoptera captured totaled 26 species in nine genera (Figs. 1–6, 7A–D), all of which belonged to tribe Rutelinae, subtribe Hopliini (Scarabaeidae).

Table 2. Floral characteristics and voucher data for species pollinated by hopliine beetles, including shape, perianth color and marking, presence of nectar, anther color, and flowering time. Abbreviations: b = bowl, f = funnel-shaped, s = salverform, + = presence, - = absence, ± = polymorphic in different populations, tr = trace amount too little to measure volumetrically. Plants collected by P. Goldblatt without voucher are indicated by the abbreviation n/v; voucher numbers are those of P. Goldblatt.

	Flower		Beetle marks	Nectar	Anther/ pollen color	Flowering time	Voucher number
	Shape	Color					
Hyacinthaceae							
<i>Daubenya</i>							
<i>aurea</i> Lindl.	b	red	—	—	yellow	Sep.	n/v
<i>Ornithogalum</i>							
<i>dubium</i> Houtt.	s	white	+	tr	white	Sep.—Nov.	n/v
<i>thyrsiflora</i> Jacq.	s	white	+	tr	white	Sep.—Nov.	n/v
Hypoxidaceae							
<i>Spiloxene</i>							
<i>capensis</i> (L.) Garside	s	cream	+	—	yellow	Aug.—Sep.	n/v
<i>serrata</i> (Thunb.) Garside	s	yellow	—	—	yellow	Aug.—Oct.	n/v
Iridaceae: Iridoideae and Nivenioideae							
<i>Aristea</i>							
<i>biflora</i> Weim.	s	mauve	+	—	orange	Aug.—Sep.	8898
<i>cantharophila</i> Goldblatt & J. C. Manning	s	cream/lilac	+	—	orange	Aug.	10284
<i>teretifolia</i> Goldblatt & J. C. Manning	s	lilac	+	—	orange	Aug.—Sep.	10250
<i>lugens</i> Ker Gawl.	s	white/blue	+	—	orange	Sep.—Oct.	10311
<i>Homeria</i>							
<i>bifida</i> L. Bolus	s	pink	—	tr	yellow	Sep.—Oct.	3969
<i>elegans</i> (Jacq.) Sweet	b	yellow	+	—	yellow	Sep.	10255
<i>ochroleuca</i> Salisb.	b	yellow	—	tr	yellow	Aug.—Oct.	10248
<i>vallisbelli</i> Goldblatt	b	yellow/pink	—	tr	yellow	Sep.—Oct.	4032
<i>Moraea</i>							
<i>bellendenii</i> (Sweet) N. E. Br.	b	yellow	+	—	yellow	Sep.—Oct.	n/v
<i>insolens</i> Goldblatt	s	orange	+	—	orange	Sep.	4880
aff. <i>M. lurida</i> Ker Gawl.	b	white	+	—	red	Aug.—Sep	10281
<i>villosa</i> (Ker Gawl.) Ker Gawl.	g	purple	+	—	orange	Sep.	6275
Iridaceae: Ixioideae							
<i>Babiana</i>							
<i>rubrocyanea</i> (Jacq.) Ker Gawl.	b	blue/red	+?	tr	brown	Sep.	n/v
<i>Hesperantha</i>							
<i>falcata</i> (L.f.) Ker Gawl.	s	yellow	—	tr	yellow	Sep.	n/v
<i>vaginata</i> (Sweet) Goldblatt	b	yellow	+	?	yellow	Sep.	4035
<i>Gladiolus</i>							
<i>meliusculus</i> (G. Lewis) Goldblatt & J. C. Manning	g	pink	+	+	yellow	Sep.	10386A
<i>Ixia</i>							
<i>curta</i> Andrews	s	orange	+	—	yellow	Sep.—Oct.	10358
<i>dubia</i> Vent.	s	orange	±	—	yellow	Sep.—Oct.	10338
<i>framesii</i> L. Bolus	s	orange	+	tr	yellow	Sep.	10333
<i>maculata</i> L.	s	orange	+	—	yellow	Sep.—Oct.	10349
cf. <i>polystachya</i> L.	s	cream	+	—	blackish	Oct.—Nov.	10568
<i>Romulea</i>							
<i>eximia</i> de Vos	b	red	+	—	yellow	Sep.	10361
<i>monadelpha</i> (Sweet) Bak.	b	red	+	—	yellow	Sep.	4036
<i>montana</i> Schltr. ex Bég.	b	yellow	—	—	yellow	Aug.—Sep.	n/v

Table 2. Continued.

	Flower		Beetle marks	Nectar	Anther/ pollen color	Flowering time	Voucher number
	Shape	Color					
<i>obscura</i> Klatt	b	red	+	—	yellow	Sep.	10317
<i>sabulosa</i> Schltr. ex Bég.	b	red	+	—	yellow	Aug.–Sep.	n/v
<i>subfistulosa</i> de Vos	b	red	+	?	yellow	Sep.	10305
<i>Sparaxis</i>							
<i>elegans</i> (Sweet) Goldblatt	s	salmon	+	tr	brown	Sep.	4286
<i>grandiflora</i> (D. Delaroche) Ker Gawl.	b	yellow	—	tr	yellow	Aug.–Sep.	2438
<i>pillansii</i> L. Bolus	s	red	+	tr	yellow	Oct.	327
<i>Thereianthus</i>							
<i>racemosus</i> (Klatt) G. Lewis	s	blue	—	—	blue	Nov.	10454
<i>Tritonia</i>							
<i>crocata</i> subsp. <i>hyalina</i> (L.f.) de Vos	b	orange	+	tr	yellow	Sep.–Oct.	n/v
<i>deusta</i> (Aiton) Ker Gawl.	b	orange	+	—	yellow	Oct.	10782
<i>squalida</i> (Aiton) Ker Gawl.	b	pink	—	tr	white	Oct.	9790
Campanulaceae							
<i>Wahlenbergia</i>							
<i>capensis</i> (L.) A. DC.	s	blue	+	?	blue	Sep.–Oct.	n/v
<i>Prismatocarpus</i>							
<i>pedunculatus</i> (Bergius) A. DC.	s	cream	—	—	cream	Oct.–Nov.	10569
Droseraceae							
<i>Drosera</i>							
<i>cistiflora</i> L.	s	cream/pink	+	—	orange	Aug.–Oct.	10282
<i>pauciflora</i> DC.	s	cream/pink	+	—	orange	Aug.–Oct.	10283

These beetles ranged in length from 6 to 14 mm. Body hairiness varied among genera and species, with *Anisonyx* having the densest and longest hairs (e.g., Figs. 1, 2, 4). The shortest beetles were *Heterochelus arthriticus* (collected on *Ixia dubia*) and *Lepthrix stigma* (collected on *Romulea sabulosa*); the longest were *Anisonyx ursus*, collected on *Drosera cistiflora*. A total of one to five beetle species were captured on 40 species of herbs in four families (Table 3). *Ixia maculata* was the only species recorded with as many as five beetle species on its flowers. Less than half (40%) of the plant species, however, were consistently visited by just one species of beetle (Table 3).

BEETLE FORAGING BEHAVIOR

Monkey beetles are common on warm days in late winter and spring when ambient temperatures are above 18°C. Individual beetles were observed in flight as early as 9.30 hr and as late as 16.00 hr, but peak activity on flowers was between 11.00 and 15.00 hr. Monkey beetles fly slowly and over relatively short distances. Beetle populations ap-

peared to be most dense on inflorescences of Asteraceae and the larger flowers of Aizoaceae subfam. Mesembryanthemoideae. In contrast, beetles captured on the flowers of species listed in Table 2 rarely occurred in groups of more than two or three per flower. In these flowers, beetles were most often seen either foraging on pollen directly on the anthers or pushing their heads into the flower center, leaving the posterior portion of their abdomens prominently displayed. Since the anthers are usually positioned close to the center of the flower and above the beetle marks on the perianth, foraging beetles were usually observed positioned on the beetle marks while they fed.

When more than one beetle of the same species was present on a flower, they often displayed intra-specific agonistic behavior, and one or more of the beetles might be driven off as a result. The beetles also used the flowers as sites to assemble and copulate. Compared to other pollinators, beetle visits to flowers lasted a long time, at least several minutes, or more when mating or evidently at rest. Beetles were often observed moving both to another



Figures 1–6. Hopliine beetles foraging on flowers. —1. *Anisonyx longipes* on *Aristea lugens*. —2. *Anisonyx ursus* on *Drosera cistiflora*. —3. *Anisochelus inornatus* on *Homeria vallisbelli*. —4. *Anisonyx ursus* on *Moraea* cf. *lurida*. —5. *Pachynema tibialis* on *Tritonia crocata* subsp. *hyalina*. —6. *Lepisia* sp. on *Hesperantha vaginata*. Arrows indicate stigmas of flowers.

flower of the same species and to flowers of different species.

Beetle contact with stigmas occurred in one of two ways depending on the length and position of the style. In *Aristea* spp. and *Drosera cistiflora* and *D. pauciflora* (Figs. 1, 2) the style is twisted to lie parallel to, and above, the perianth surface. The stigmatic areas are thus removed from the center of the flower. In this case, beetles brushed against the stigma or crawled over it when they moved across the flower. In the second, more common, case the style is short and the stigma barely protrudes beyond the short floral tube or cup. The beetle contacted the stigma ventrally while crawling over it or dorsally when climbing into the floral cup, while either foraging or engaging in agonistic or copulatory behavior. As the color of the pollen is often so distinctive and contrasts so sharply with that of the beetles and the stigmas, pollen could easily be seen clinging to the hairs of the beetles and on the stigmas after the beetles departed. The style branches of *Moraea* species are broad and arching, concealing the anthers on their abaxial surfaces (Fig. 4). *Moraea* pollen was deposited on the abaxial stigmatic lobe only when a beetle dusted with pollen crawled under a style branch to lie in the center of the flower. The prominent "nectar guides" and dark tepal claws in some species of *Moraea* may in fact be beetle marks encouraging these insects to move into the center of the flower directly under the gynandrium to contact both pollen and stigmas. As female beetles continued to feed while mating, both males and females sometimes became dusted with pollen and brushed against stigmas.

POLLEN LOAD ANALYSES

A total of 294 monkey beetles were collected on 40 species of flowering herbs (Table 3) representing 14 genera. More than 90% (270) of the beetles carried the pollen of the host flower on which they were collected. However, of these only 28% carried their host plant's pollen exclusively (Table 3). The majority of beetles carried a minimum of two and a maximum of five recognizable pollen taxa on their bodies. The only beetle to carry five pollen taxa was an individual of *Pachynema crassipes*, 10 mm long, collected on *Gladiolus meliusculus*, which had the pollen of *G. meliusculus*, *Romulea eximia*, *Drosera cistiflora*, *Spiloxene capensis*, and an unidentified member of the Asteraceae clinging to its body surface.

Pollen washes showed that 28 beetles each carried pollen of more than one species of Iridaceae.

Of these, four specimens of *Anisonyx longipes*, collected on *Aristea lugens*, each carried pollen of three species of Iridaceae: *A. lugens*, *Geissorhiza ?aspera* Goldblatt, and *Moraea villosa*.

OTHER VISITORS

In *Sparaxis elegans*, *S. grandiflora*, and *S. pillansii*, beetle species (Table 3) appeared to share flowers with the tabanid fly, *Philoliche atricornis*. In contrast to the flower-visiting *Philoliche gulosa* and *P. rostrata* (Goldblatt et al., 1995; Manning & Goldblatt, 1997), which have mouth parts 20–30 mm long, *P. atricornis* has a proboscis only 3–5 mm long. This fly appeared to forage on the flowers of *Sparaxis* species for nectar exclusively, and carried ample quantities of pollen of the host flower, which in *S. elegans* and *S. pillansii* is a distinctive red-brown color, easily visible to the naked eye as the flies foraged or flew from flower to flower (Table 4).

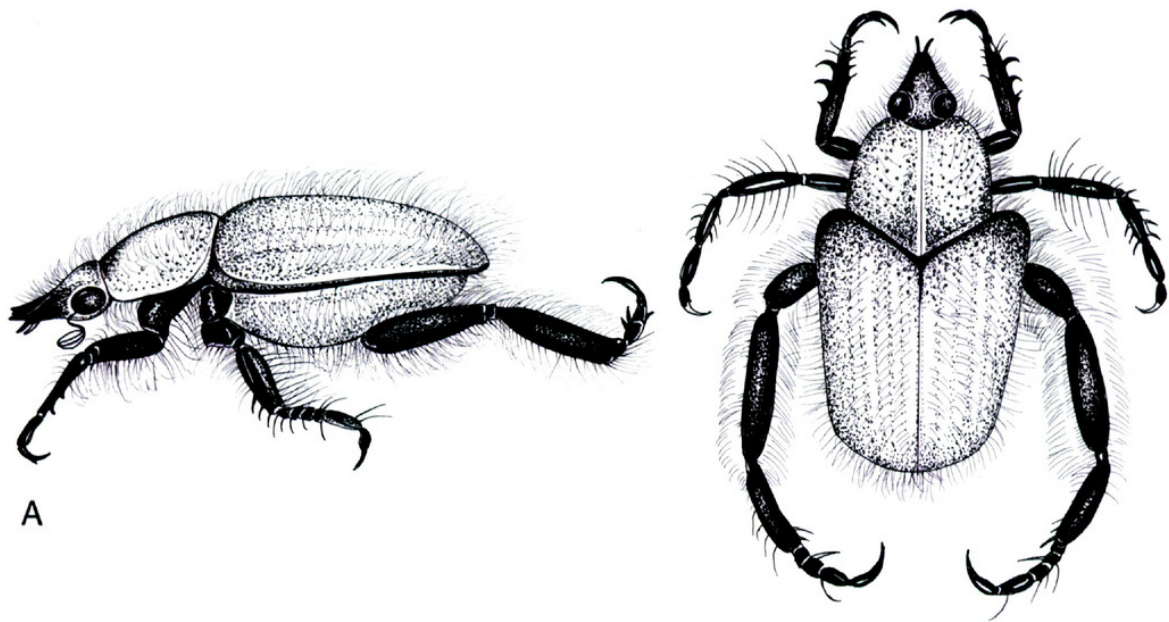
Ixia framesii and *Ornithogalum thyrsiflora* are visited by both the beetle *Lepithrix ornatella* and the tabanid, *Philoliche atricornis*. It also forages for nectar and carries the pollen of both host flowers (Tables 3, 4).

The beetle *Peritrichia pseudoplebia* may share *Homeria elegans* with the muscid fly *Orthellia* sp. and the native honey bee, *Apis mellifera*, all of which may contact the stigmas of *H. elegans* and transport its pollen (Table 4). *Homeria ochroleuca* receives the most diverse assembly of floral foragers. The beetle *Anisonyx ursus* may share the flowers with *Apis mellifera* and as many as six dipteran taxa. However, the particularly large anthers, prominent beetle marks, and depauperate nectar of flowers of *H. elegans* suggest that beetle pollination is more important in that species than in *H. ochroleuca*, with its wider range of visitor species and more ample nectar production.

Gladiolus meliusculus, *Romulea subfistulosa*, and *Daubenya aurea* are visited by a combination of hopliine beetles and solitary bees in the families Andrenidae and Halictidae (Tables 3, 4), and *Aristea biflora* Weim. by hopliine beetles and occasionally by *Apis mellifera*. All three bees, *Andrena* sp. (Andrenidae), *Patellapis* sp. (Halictidae), and *Apis mellifera*, appear to be polylectic foragers, but they do contact the stigmas of their respective flowers.

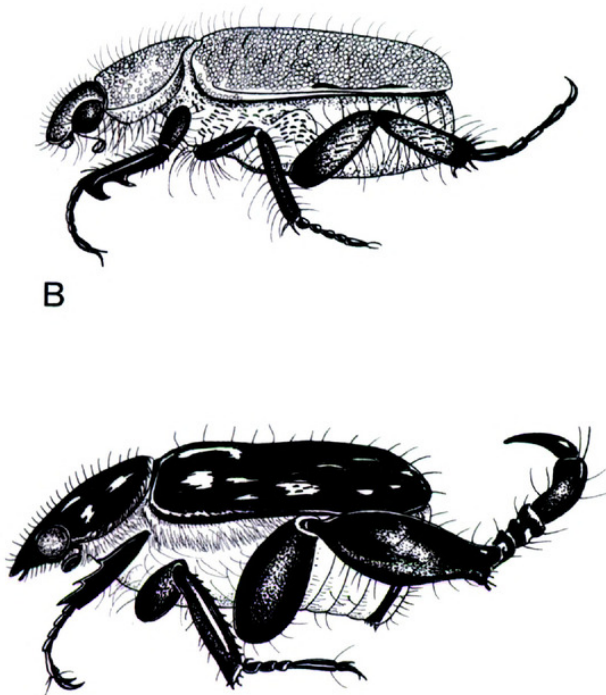
LOCAL FLORAL GUILDS

At some study sites, there was a tendency for floral pigmentation patterns to converge. This was striking at Sir Lowry's Pass, where *Aristea cantharophila*, *Drosera cistiflora*, *D. pauciflora*, and *Moraea*

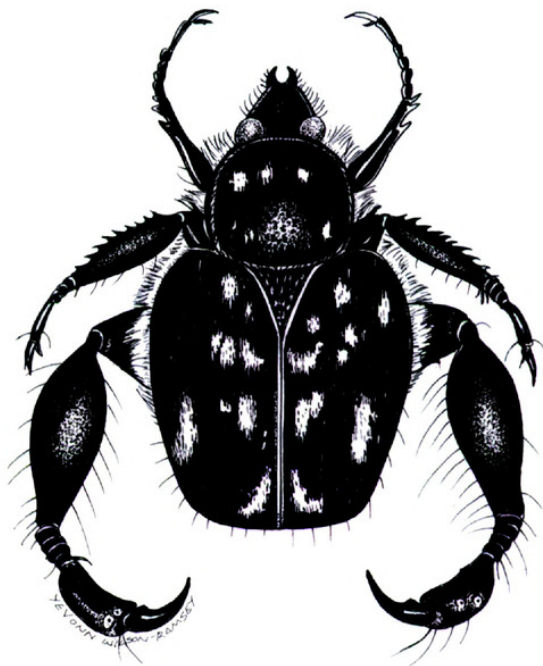


A

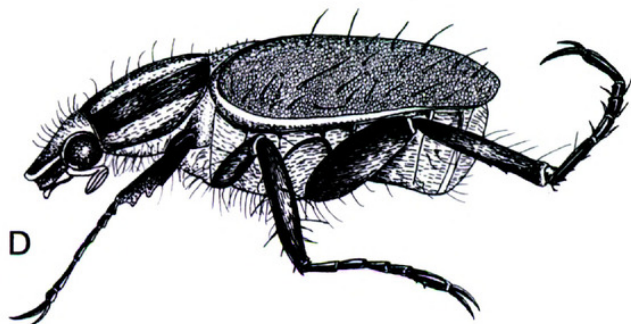
B



C



D



sp. aff. *lurida* all had cream or lilac flowers with dark centers and orange pollen. At Malmesbury commonage, *Aristea lugens* and *Moraea villosa* flowers were blue to mauve with very dark markings on the outer tepals. Near Caledon, *A. biflora*, *Drosera pauciflora*, and *Spiloxene capensis* all had whitish to pale mauve, salver-shaped flowers with dark markings near the center. Along the Bokkeveld Escarpment, yellow-flowered species dominated the beetle-pollinated guild that includes *Homeria valisbelli*, *Romulea montana*, and *Spiloxene serrata*, as well as other small-flowered dicots including *Ursinia* sp. (Asteraceae) and *Oxalis obtusa* Jacq. At other sites obvious color convergence is not evident, and color patterns are broadly mixed. For example, at sites on the Bokkeveld Plateau, *Romulea monadelphica* and *R. sabulosa* have dark red and black flowers, those of *Hesperantha vaginata* are deep yellow and chocolate, and those of *Sparaxis elegans* and *S. pillansii* are pink to salmon with dark red or purple and yellow markings.

DISCUSSION

Pollination by hopliine monkey beetles obviously conforms to a pattern distinct from classical cantharophily in the magnoliid angiosperms. In particular, flowers and inflorescences in the pollination systems described above do not have urn-like, haplomorphic perianths or overlapping bracts. Pollination by monkey beetles in southern Africa more closely parallels beetle pollination by the large scarabs, buprestids, and cerambycids in Australia and the eastern Mediterranean. Perianths are usually open and shallow, anthers do not extrude or shed pollen, and strong odors are uncommon. In fact, similarities between the red-flower guild of the eastern Mediterranean and the monkey-beetle flowers of southern Africa are particularly marked. Bright orange to red colors, salver-shaped flowers, and absence of floral odor are well distributed in the beetle flowers of southern Africa and the dark, beetle-like marks of the southern African species may be comparable to the blackened stamens or blackened tepal bases in some of the Mediterranean flowers. Few of these flowers, however, appear to secrete nectar as do the Mediterranean species of *Anemone*, *Ranunculus*, and *Tulipa*.

A primary difference between beetle pollination in the Mediterranean and in southern Africa is the

taxonomic diversity of the Coleoptera involved. In the Mediterranean, pollination of the red-flower guild involves only six species of the genus *Amphicoma* (Dafni et al., 1990). The southern African guild of beetle pollinators is far broader, with at least nine genera of floral foragers representing a total of over 20 species.

Our results suggest that plant species visited by Hopliini may be specialized for beetle pollination to varying degrees. Thus, where plants offer nectar in shallow floral bowls, generalist entomophily occurs and beetles are members of a wider pollinator spectrum that includes native Diptera, Hymenoptera, and sometimes Lepidoptera. This would appear to be the most likely scenario in *Homeria elegans*, *H. ochroleuca*, *Gladiolus meliusculus*, *Ixia framesii*, *Sparaxis elegans*, *S. grandiflora*, and *S. pillansii*. Pollination by a range of different organisms is known in many flowers; for example, some plant species in the Western Hemisphere and in Australia are pollinated by a combination of birds and bees (Armstrong, 1979). In southern Australia the flowers of a number of woody genera appear to be pollinated by a combination of syrphid flies and small colletid bees (Bernhardt, 1989). Pollination strategies combining beetles and other insects are perhaps less well known, but may be much more common than previously anticipated. For example, Schneider and Buchanan (1980) found that the magnoliid flowers of *Nelumbo lutea* are pollinated by a combination of bees, flower flies, and cantharid beetles. It would appear that monkey beetles are a predictable part of generalist entomophily in the flora of southern Africa, much as syrphid flies and small colletid bees are a dominant part of generalist entomophily in southern Australia (Bernhardt, 1989). In other instances, however, monkey beetles appear to be the sole pollinators and flowers are highly specialized for beetle pollination.

The high incidence of pollination by monkey beetles among the Iridaceae of southern Africa has not been widely appreciated. The literature dealing with pollination ecology of the Iridaceae has emphasized the prominent role of bees, moths, birds (Knuth, 1909; Vogel, 1954), and nectarivorous flies with moderate to long mouth parts (Goldblatt & Bernhardt, 1990; Goldblatt et al., 1995; Manning & Goldblatt, 1996, 1997). However, work by Picker and Midgley (1996), Steiner (1998), and our own

Figure 7. Dorsal and/or lateral views of hopliine beetles. —A. *Peritrichia subsquamosa*. —B. *Lepisia rupicola*. —C. *Pachycnema crassipes*. —D. *Lepisia* sp. (Nieuwoudtville). Scale bar = 5 mm. (Drawn by Y. Wilson-Ramsey.)

Table 3. Pollen load analysis of collected beetles.

Plant and beetle taxon	Number of beetles carry- ing pollen load(s)			
	Host flr only	Host flr + other sp.	Other sp. only	No pol- len
IRIDACEAE				
<i>Aristea</i>				
<i>biflora</i>				
<i>Anisonyx lepidotus</i>	1	2	0	0
<i>cantharophila</i>				
<i>Anisonyx ursus</i>	0	3	0	0
<i>Peritrichia pseudoplebeia</i>	0	9	0	1
<i>lugens</i>				
<i>Anisonyx longipes</i>	1	9	0	0
<i>A. ursus</i>	1	9	0	0
<i>Lepithrix ornatella</i>	2	1	0	0
<i>teretifolia</i>				
<i>Petririchia pseudoplebeia</i>	1	2	0	0
<i>Babiana</i>				
<i>rubrocyanea</i>				
<i>Pachynema crassipes</i>	0	1	0	3
<i>Gladiolus</i>				
<i>meliusculus</i>				
<i>Lepisia rupicola</i>	2	4	0	1
<i>Pachynema crassipes</i>	0	6	0	0
<i>hirsutus</i>				
<i>Anisonyx ursus</i>	0	1	0	1
<i>Hesperantha</i>				
<i>falcata</i>				
<i>Peritrichia pseudoplebeia</i>	1	0	0	0
<i>vaginata</i>				
<i>Lepisia</i> sp. 1	7	5	0	0
<i>Homeria</i>				
<i>elegans</i>				
<i>Peritrichia pseudoplebeia</i>	6	0	0	1
<i>ochroleuca</i>				
<i>Anisonyx ursus</i>	2	0	0	0
<i>vallisbelli</i>				
<i>Anisochelus inornatus</i>	3	5	0	1
<i>Ixia</i>				
<i>curta</i>				
<i>Lepisia rupicola</i>	0	3	0	0
<i>Lepithrix fulvipes</i>	0	5	0	0
<i>Pachynema crassipes</i>	0	1	0	0
<i>dubia</i>				
<i>Heterochelus arthriticus</i>	3	2	0	0
<i>Lepithrix ornatella</i>	0	1	0	0
<i>Pachynema crassipes</i>	0	2	0	0
<i>framesii</i>				
<i>Lepithrix ornatella</i>	0	5	0	1
<i>maculata</i>				
<i>Heterochelis sexlineatus</i>	0	2	0	0
<i>Lepithrix longitarsis</i>	2	2	0	0
<i>L. ornatella</i>	0	5	0	0

Table 3. Continued.

Plant and beetle taxon	Number of beetles carry- ing pollen load(s)			
	Host flr only	Host flr + other sp.	Other sp. only	No pol- len
<i>Pachynema crassipes</i>	0	2	0	0
<i>Scelophysa ornatella</i>	0	1	0	0
<i>monadelpha</i>				
<i>Lepithrix fulvipes</i>	0	1	0	0
<i>polystachya</i>				
<i>Peritrichia subsquamosus</i>	0	3	0	0
<i>Moraea</i>				
<i>bellendenii</i>				
<i>Heterochelus unguicu- latus</i>	1	3	0	1
<i>insolens</i>				
<i>Anisonyx lepidotus</i>	1	1	0	0
<i>aff. lurida</i>				
<i>A. ursus</i>	3	4	2	1
<i>Peritrichia pseudoplebeia</i>	0	6	0	0
<i>villosa</i>				
<i>Anisonyx longipes</i>	1	6	0	0
<i>A. ursus</i>	0	3	1	0
<i>Romulea</i>				
<i>eximia</i>				
<i>Lepisia rupicola</i>	0	4	0	0
<i>Pachynema crassipes</i>	0	4	0	0
<i>monadelpha</i>				
<i>Lepisia</i> sp. 1	6	8	0	3
<i>sabulosa</i>				
<i>Anisochelus inornatus</i>	3	3	0	0
<i>Lepithrix stigma</i>	0	5	1	0
<i>subfistulosa</i>				
<i>Lepisia</i> sp. 2	0	7	0	0
<i>Sparaxis</i>				
<i>elegans</i>				
<i>Lepisia</i> sp. 1	1	5	0	0
<i>Anisochelus inornatus</i>	0	5	1	0
<i>grandiflora</i>				
<i>Peritrichia rufotibialis</i>	0	2	0	0
<i>Anisochelus inornatus</i>	2	4	0	0
<i>Peritrichia</i> sp. 1	0	2	0	0
<i>pillansii</i>				
<i>Lepisia</i> sp. 1	1	7	1	1
<i>Thereianthus</i>				
<i>racemosus</i>				
<i>Khoina bilateralis</i>	2	1	0	1
<i>Tritonia</i>				
<i>deusta</i>				
<i>Peritrichia hybrida</i>	3	0	0	0
<i>hyalina</i>				
<i>Pachynema tibialis</i>	0	6	0	0
<i>squalida</i>				
<i>Peritrichia</i> sp. 2	7	2	0	0

Table 3. Continued.

Plant and beetle taxon	Number of beetles carrying pollen load(s)			
	Host flr only	Host flr + other sp.	Other sp. only	No pollen
HYACINTHACEAE				
<i>Ornithogalum dubia</i>				
<i>Peritrichia subsquamosus</i>	1	2	0	0
<i>thyrsoideis</i>				
<i>Lepithrix fulvipes</i>	1	0	0	0
<i>L. longitarsis</i>	0	2	0	0
<i>P. crassipes</i>	0	1	0	0
<i>Daubenya aurea</i>				
<i>Lepisia</i> sp. 2	0	3	0	0
DROSERACEAE				
<i>Drosera cistiflora</i>				
<i>Anisonyx ursus</i>	3	1	0	0
<i>pauciflora</i>				
<i>Anisonyx lepidotus</i>	1	2	0	0
CAMPANULACEAE				
<i>Prismatocarpus pedunculatus</i>				
<i>Pachynema saga</i>	0	3	0	0
<i>Peritrichia subsquamosus</i>	3	1	1	0
<i>Wahlenbergia capensis</i>				
<i>Lepisia</i> sp.	3	0	1	0
Total	75	195	8	16

research indicates that beetle pollination must now be accepted as being widespread in the southern African flora. This is especially marked in Iridaceae, which have undergone their greatest adaptive radiation and speciation in western southern Africa, where flower-visiting Hopliini show their greatest diversity.

Modification of the irid flower for pollination primarily by monkey beetles has occurred in several genera with diverse floral morphology. In most, the shift seems to be relatively minor, based more on morphological reduction than enlargement. This applies particularly to genera in which an actinomorphic, bowl-shaped flower is ancestral, including *Hesperantha*, *Homeria*, *Ixia*, *Moraea*, and *Romulea*. In a few genera with primitively zygomorphic flowers, change in symmetry has been necessary; for example, in *Sparaxis* and *Tritonia* the adaptive shift has been more pronounced. The Iridaceae pollinated by monkey beetles are more likely to have

Table 4. Pollen load analysis of insects collected on the same species as beetles. Taxonomic affiliations are as follows: Diptera: *Philoliche* (Tabanidae); *Orthellia* (Muscidae); *Scathophaga* (Sarcophagidae). Hymenoptera–Apidae: *Andrena* (Andrenidae); *Apis* (Apidae); *Patellapis* (Halictidae).

Plant and insect taxon	Number of insects carrying pollen load(s)			
	Host flr only	Host flr + other sp.	Other sp. only	No pollen
<i>Gladiolus meliusculus</i>				
<i>Andrena</i> sp.	0	2	0	0
<i>Homeria elegans</i>				
<i>Apis mellifera</i>	2	0	0	0
<i>Orthellia</i> sp.	0	2	0	1
<i>Scathophaga stercoraria</i>	0	0	0	3
<i>ochroleuca</i>				
<i>Anthomyia</i>	0	0	0	1
<i>Apis mellifera</i>	3	1	0	0
Calliphoridae	0	0	1	0
<i>Orthellia</i> sp.	5	0	0	0
<i>Musca</i> sp.	0	2	0	1
<i>Scathophaga stercoraria</i>	0	2	0	3
<i>Syrphidae</i>	0	1	0	0
<i>Ixia framesii</i>				
<i>Philoliche atricornis</i>	3	3	0	0
<i>Moraea</i>				
aff. <i>lurida</i>				
? <i>Musca</i> sp.	1	0	0	0
<i>Romulea subfistulosa</i>				
<i>Patellapis</i> sp.	0	2	0	0
<i>Sparaxis elegans</i>				
<i>Philoliche atricornis</i>	0	6	0	0
<i>grandiflora</i>				
<i>Philoliche atricornis</i>	0	3	0	0
<i>Patellapis</i> sp.	0	3	0	0
<i>pillansii</i>				
<i>Philoliche atricornis</i>	0	2	0	0
Total	14	29	1	9

prominent, dark nectar guides and produce less nectar than the African Iridaceae pollinated by long-tongued bees, flies, or other insects (Goldblatt et al., 1995; Manning & Goldblatt, 1996, 1997). In Iridaceae subfam. Ixiioideae, which is characterized by the presence of a perianth tube, the tube is also reduced in some way in monkey beetle pollinated species, either in length or diameter, resulting in a

role change from nectar reservoir to pseudopedicel. Flowers pollinated by long-tongued flies in southern Africa also typically lack a discernible scent, e.g., *Gladiolus*, *Lapeirousia*, *Nivenia* (Goldblatt, 1993; Goldblatt & Manning, 1998; Manning & Goldblatt, 1995, 1996, 1997). The main features that distinguish species of Iridaceae as having beetle-pollinated flowers appear to be the distinctive beetle-like marks often combined with particularly bright flower colors, which have evolved convergently in many other families; a reduction in the amount of nectar produced; and floral actinomorphy. Salver- to shallow bowl-shaped perianths are also a frequent aspect of this syndrome.

Adaptive radiation in response to monkey-beetle pollination is evident in some lineages within several genera of the Iridaceae, most conspicuously in *Ixia* sect. *Ixia*. Nearly all members of that section have spreading tepals, contrasting central marks, a filiform perianth tube, and lack nectar. The tube is blocked by the style and the mouth is closed off by the central filaments that are either coherent or united. Some 20 species are currently included in section *Ixia*, out of a total of 50 species in the genus (Lewis, 1962; de Vos, 1988). Most other species of the genus have campanulate or cylindric perianth tubes that contain nectar in the lower part, which is accessible to nectar-foraging insects (Lewis, 1962; Manning & Goldblatt, 1997, and unpublished data), but at least *I. framesii* (sect. *Morphixia*) is also visited by monkey beetles. In *Sparaxis* and *Tritonia*, floral zygomorphy is most likely ancestral (based on outgroup comparison, Goldblatt & Manning, unpublished), but zygomorphic flowers or at least zygomorphic perianths characterize species pollinated by monkey beetles or a combination of these beetles and *Philoliche atricornis*. In these species, the perianth tube is also filiform and blocked by the style and appears to function only as a stalk for the flower. The actinomorphic, beetle-pollinated flowers of these species appear to be derived in both genera, an unexpected phenomenon.

Pollination in *Moraea* is, as far as recorded, predominantly by bees (Goldblatt et al., 1989), but pollination by monkey beetles has been documented by Steiner (1998) within subgenus *Vieusseuxia*, notably *M. villosa*. Several allied species, loosely called peacock moraeas (for their prominent dark tepal markings often with a central pale eye), also have flowers that do not produce nectar, and in addition often have a sterile flap of tissue at the base of the large outer tepal, the limb of which is broad and outspread. This lineage includes some eight species, of which at least *M. gigandra* L. Bolus, *M. neopavonia* R. Foster, *M. tulbaghensis* L. Bolus, and

M. villosa have flowers adapted for monkey-beetle pollination. Our observations on *M. villosa* mirror Steiner's conclusions. Other species of this apparently monophyletic group include *M. amissa* Goldblatt, *M. calcicola* Goldblatt, and *M. loubseri* Goldblatt, also likely, on the basis of their floral pigmentation, to be pollinated by beetles. Our own observations show that monkey-beetle pollination in *Moraea* is not confined to this group of species. At least *M. bellendenii*, *M. insolens*, and the new taxon here allied to *M. lurida* also appear to be adapted for monkey-beetle pollination, and according to Scott Elliot (1891), so does *M. tricuspidata* (L. f.) G. J. Lewis. *Moraea lurida* itself has flowers with livid red tepals, sometimes marked with yellow, a fetid odor, and which produce nectar on the tepal claws. The flowers in our study population were whitish with small yellow nectar guides, dark style branches, and produced neither noticeable odor nor nectar. In other respects, the plants appear similar to *M. lurida*.

In *Aristea*, four of the seven species of section *Pseudaristea* currently recognized have flowers adapted in different ways for monkey-beetle pollination. The ancestral condition in the genus is pollination by pollen-collecting female bees (Goldblatt & Manning, 1997), and the species of all other sections have dark blue tepals, small yellow anthers, and yellow pollen, including as well *A. pauciflora* Wolley-Dod of section *Pseudaristea*. Four species of section *Pseudaristea* have whitish, pale blue, or lilac tepals with contrasting markings and elongate anthers with orange pollen, and beetle pollination has now been recorded for all of them (Table 3). Even at sites where beetles were not observed foraging on *Aristea* flowers, pollen washes have shown ample quantities of distinctive *Aristea* pollen, indicating visits to species. For example, the beetle *Anisonyx lepidotus*, collected on *Moraea insolens*, showed the presence of pollen of coblooming *A. biflora*, which grew nearby.

The situation in *Romulea* also suggests that radiation and speciation based on monkey-beetle pollination are fundamental to the genus. Most of the approximately 80 species of *Romulea* in the southern African winter-rainfall zone have bowl-shaped flowers and a perianth tube with a filiform base, and many have beetle-like marks (de Vos, 1972). Pollinators of these species are either monkey beetles exclusively, or a combination of beetles and pollen-collecting bees (Apidae, Halictidae), or in some instances (e.g., *R. flava*, the flowers of which lack markings) possibly only bees (Goldblatt et al., unpublished data).

The floristic diversity of the Cape Floristic Re-

gion is greater than that of such Mediterranean regions as the California Floristic Province, Central Chile, and southwestern Australia (Goldblatt, 1997). One reason for this diversity may be that beetle pollinators have acted, and may continue to act, as unusually powerful mechanisms of natural selection as plant populations become isolated due to dispersal and/or vicariance.

Why do monkey beetles, in particular, appear to play such an important role in the radiation of the flora, since they lack the long, specialized mouth parts and rapid flying speeds of large, long-tongued flies and bees (Goldblatt & Bernhardt, 1990; Goldblatt et al., 1995)? The answer may be that monkey beetles, for all their apparent limitations, are opportunistic foragers that contact flower stigmas, just like nemestrinid flies and anthophorid bees. Our collections suggest that the majority of beetle-pollinated geophytes may depend on only one or two beetle species to effect pollination. However, no beetle species appears dependent on the flowers of any single geophyte species as a food source or mating site. This is reflected further by the fact that the overwhelming majority of beetles carry mixed loads of pollen. Consequently, while monkey beetles probably find levels of floral diversity adequate, we suggest that the geophytic flora finds the density of beetle pollinators less so. This presumably results in competition between geophytic species for the limited pollinator resource, e.g., fruit set in many species of the Cape Flora is known to be pollinator-limited (Johnson & Bond, 1997). Speciation in the geophytic members of the Cape Flora may thus be driven, in part, by this competition.

Floral morphology in the monkey-beetle pollinated species of the Cape Flora seems conservative, while scent and nectar production are negligible. These floral trends become comprehensible in the light of beetle morphology and behavior. Monkey beetles lack both manipulative forelegs and elongated glossae; they do not appear to respond to floral odors, but require a flat surface to mate. Some flower scarabs may have color vision equal to, or much broader than, for example, that of bumblebees (Dafni et al., 1990). Consequently, the convergent evolution of the guild of monkey-beetle-pollinated flowers in southern Africa emphasizes flattened, radial symmetry combined with complex patterns of pigmentation and perianth colors often contrasting with colors of the anthers and/or pollen.

The pollination of flowers by monkey beetles in southern Africa appears to have shaped the flora in two ways. First, it is another factor that may help explain the unusually brilliant and broad range of floral colors and contrasting patterns in the Cape

Flora in general. Second, competition for monkey beetles as pollinators has very likely encouraged both adaptive radiation and convergent floral evolution within several plant families, in particular the Iridaceae.

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<https://doi.org/10.2307/2992006>.

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DOI: <https://doi.org/10.2307/2992006>

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