

Pollination mechanisms in the African genus *Moraea* (Iridaceae, Iridoideae): floral divergence and adaptation for pollinators

Peter GOLDBLATT

B.A. Krukoff Curator of African Botany, Missouri Botanical Garden,
P.O. Box 299, St Louis, Missouri 63166 (USA)
peter.goldblatt@mobot.org

Peter BERNHARDT

Department of Biology, St Louis University, St Louis, Missouri 63103 (USA)
bernhap2@slu.edu

John C. MANNING

Compton Herbarium, National Botanical Institute,
Private bag X7, Claremont 7735 (South Africa)
manning@nbict.nbi.ac.za

ABSTRACT

Field observations, floral dissections, and pollen load analyses of insects captured on 35 species of *Moraea* (total 195 spp.), combined with past pollination studies on 16 more help identify five main floral types within this pan-African and Eurasian genus of Iridaceae. Most species are cross-pollinated by a narrow range of insects while a few are facultatively autogamous. Floral type determines whether a species is pollinated primarily by Coleoptera, Diptera, or Hymenoptera. Most common are flowers of the *Iris*-type, probably ancestral, that consist of three functionally separate bilabiate units (meranthia), each resembling one gullet flower. They are pollinated by a range of medium-sized to large bees of several families. Specialized adaptations related directly to the pollination system include reduction in the length of the tepal claws, enlargement of the outer tepal limbs, and acquisition of "beetle" marks combined with loss of nectar and scent, which shift the mode of pollination from the ancestral meranthium bee-pollinated type to painted bowl-beetle pollination using hopliine scarab beetles. Likewise, reduction in size of the style branches in conjunction with the loss of distinction between the inner and outer tepal whorls results in a cup- or bowl-like perianth, which combined with changes in floral odor favor more generalist systems including small bees, hopliines and flies, or flies exclusively. The shortening of the tepal claws together with the prominent display of pollen on an exaggerated column, leads to an active pollination system exploiting female bees of several families that harvest pollen to feed their offspring.

KEY WORDS

Iridaceae,
Moraea,
pollination biology,
Hymenoptera,
Apidae,
Diptera,
Coleoptera,
Hopliini,
floral specialization,
Cape flora.

RÉSUMÉ

Les mécanismes de pollinisation dans le genre africain Moraea (Iridaceae, Iridoideae) : divergence florale et adaptation aux pollinisateurs.

Des observations de terrain, des dissections de fleurs et des analyses de la charge pollinique d'insectes capturés sur 35 espèces de *Moraea* (195 espèces au total), combinées à des études antérieures sur la pollinisation de 16 espèces supplémentaires ont permis d'identifier cinq types floraux principaux dans ce genre d'Iridaceae pan-africain et eurasiatique. La plupart des espèces ont une pollinisation croisée assurée par quelques espèces d'insectes, alors que quelques-unes sont facultativement autogames. Le type floral détermine si une espèce est originairement pollinisée par des Coleoptera, Diptera ou Hymenoptera. La plupart des fleurs sont du type *Iris*, probablement ancestral, consistant en trois unités bilabées (meranthia) fonctionnellement séparées, chacune ressemblant à une fleur gamopétale. Elles sont pollinisées par toute une série d'abeilles, de taille moyenne à grande, et appartenant à plusieurs familles. Les spécialisations liées directement au système de pollinisation incluent le raccourcissement des onglets des tépales et l'élargissement du limbe des tépales extérieurs, ainsi que l'acquisition de signaux nouveaux parallèlement à la perte du nectar et du parfum. On passe alors du mode de pollinisation ancestral apiphile (abeilles-meranthium), au type cantharophile (coléoptères-« coupe peinte ») utilisant des Hopliinae. Des systèmes de pollinisation plus généralistes (petites abeilles, Hopliinae et mouches), tendant à une musciphilie stricte, sont également reconnus dans le genre. Ils se caractérisent par une réduction des branches stylaires, une différenciation des tépales externes et internes, formant un périanthe en tasse ou en coupe, et par un changement dans l'odeur florale. Enfin, un système de pollinisation très active, impliquant le raccourcissement des onglets tépalaire et la présentation secondaire du pollen sur une colonne très étirée, exploite des abeilles femelles de plusieurs familles butinant le pollen afin de nourrir leur progéniture.

MOTS CLÉS

Iridaceae,
Moraea,
biologie de la pollinisation,
Hymenoptera,
Apidae,
Diptera,
Coleoptera,
Hopliini,
spécialisation florale,
flore du Cap.

INTRODUCTION

As circumscribed by GOLDBLATT (1998), *Moraea* is a large genus of the predominantly Old World tribe Irideae of subfamily Iridoideae of the Iridaceae (GOLDBLATT 1990; REEVES *et al.* 2001). Comprising some 195 species, *Moraea* occurs throughout sub-Saharan Africa and has two species in the Mediterranean Basin and Middle East (GOLDBLATT 1986; GOLDBLATT & MANNING 1995, 2002a). Several allied or “satellite” genera have at times been recognized including *Barnardiella* (1 sp.), *Gynandriris* (9 spp.), *Homeria* (32 spp.), *Galaxia* (15 spp.), *Hexaglottis* (6 spp.), *Roggeveldia* (2 spp.), and *Sessilistigma*

(1 sp.) but as a result of both morphological and DNA sequence analysis all these genera are now understood to be nested within *Moraea* (GOLDBLATT 1998; GOLDBLATT *et al.* 2002a). Recognized largely by a range of floral specializations, these nested genera have flowers with modes of presentation distinct from the “*Iris*-type” flower typical of *Moraea* species, that indicate diverging pollination strategies.

Although *Moraea* species are fairly uniform vegetatively, floral variation is extensive, hence the recognition in the past of segregate genera based on floral form. The ancestral (plesiomorphic) flower, assessed by outgroup comparison, is that also found in the genera *Dietes* and *Iris*

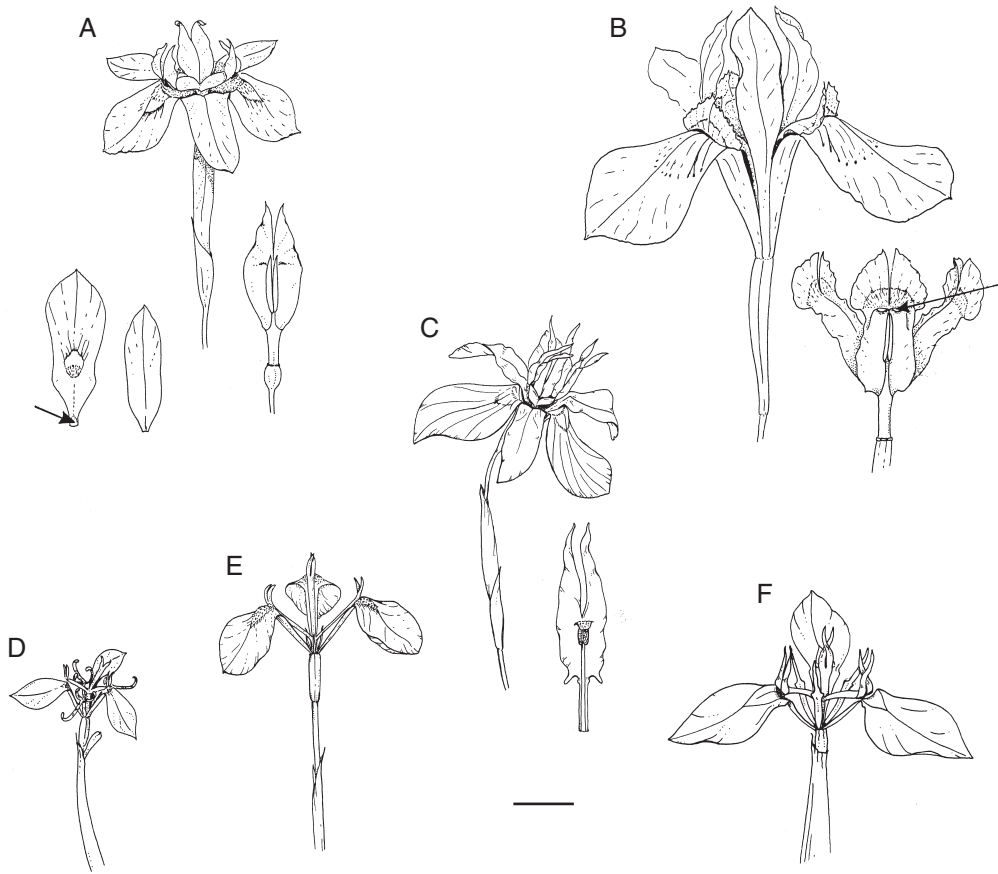


FIG. 1. — *Iris*-type flowers in *Moraea*: **A**, *M. bipartita*, whole flower and outer and inner tepal and style branch shown separately with arrow indicating the nectary on the interior (adaxial) surface of the outer tepal; **B**, *M. huttonii*, whole flower and the style branches and stamens drawn separately, arrow showing the stigmatic lobe on the abaxial surface of the style branch; **C**, *M. gawleri*, entire flower and separated style branch to show stigmatic lobe arching over the anther; **D**, *M. brevistyla* (note trilobed inner tepals); **E**, *M. tripetala*, with inner tepals reduced to minute cusps; **F**, *M. algoensis*, with reduced inner tepals. Scale bar: 1 cm for flowers, floral dissections variously enlarged. Drawn by Margo BRANCH.

(GOLDBLATT 1990; REEVES *et al.* 2001). The outer tepals are larger than the inner and strongly clawed, with the claw closely opposed to an enlarged petaloid style branch, and the spreading tepal limb is marked with a basal nectar guide (Fig. 1). The smaller inner tepals typically have an ascending claw and spreading, or less often erect, limb and usually lack markings. Perigonal nectaries are located within the flower at the base of the outer tepals. The style in such flowers is short and exceeded by three long, petal-like style branches against which the upper part of the filaments and the anthers are appressed (GOLDBLATT

1986, 1990). The partial fusion of the filaments is a synapomorphy for the clade that includes *Moraea* and its sister genus *Ferraria*, whereas *Bobartia*, *Dietes* and *Iris*, remaining genera of the tribe, have free stamens. Each style branch bears a pair of conspicuous terminal petaloid appendages (style crests), which extend above a transverse stigmatic lobe. How this basic flower organization varies is central to understanding the diverse pollination systems in the genus.

Here we describe the main flower types in *Moraea* and the chief visitors to each of these types. We compare and contrast functional floral

morphology and physiological expression (e.g., pigmentation, scent variation, and nectar secretion) that result in divergent pollination systems within the genus. Original records of flower visitors are presented here and are combined with published observations to assess and define the different pollination strategies in a limited number of “floral types” in which some characters intergrade or overlap.

METHODS

FLORAL PHENOLOGY, LIFE SPAN, AND FLORAL PRESENTATION

We present observations for 35 *Moraea* species made from 1995 to 2004 in the field and in living collections at Kirstenbosch Botanic Garden, Cape Town, South Africa. Field observations were made at various sites in southern Africa (Table 1) and include the two major climate zones of the subcontinent: the southwestern Cape and the western Karoo, South Africa, which have a Mediterranean climate with wet winters and dry summers; and the eastern half of southern Africa (Lesotho, South Africa, and Swaziland), a region of summer rainfall and relatively dry, cold winters. Observations of insect foraging involved 5–10 hours per plant species and included the recording of floral attractants (pigment patterns, scent, nectar secretion), mode and timing of anthesis (opening of individual buds, anther dehiscence, expansion of stigmatic lobes), the behavior of insect visitors to flowers, and the taxonomic diversity of floral foragers. The range of species studied includes examples from all the major flower types in the genus.

Floral scent was noted in the field and in cultivated plants. Scents too weak to be 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 were smelled after a minimum of 60 minutes (BUCHMANN 1983).

NECTAR ANALYSIS

Nectar volume measurements are difficult to determine in *Moraea* because quantities are small. Nectar sugar chemistry and concentration

were sampled using unbagged cut flowers maintained in the laboratory where insects were excluded. If nectar is sampled within 24 hours of removal of the flowering stem from the field we believe, based on previous studies using *Lapeirousia* (Iridaceae) (GOLDBLATT *et al.* 1995), that nectar volume is increased but nectar sugar chemistry and concentration are unaffected. To collect nectar a micro-capillary tube was placed over each of the nectaries of a flower in turn and nectar was withdrawn into the tube. The percentage of sucrose equivalents in fresh nectar was measured using a Bellingham and Stanley handheld refractometer (0–50%) from five or more individuals per population, unless fewer individuals were available. Additional nectar samples were dried on Whatmans filter paper No. 1 and analyzed by B.-E. VAN WYK, Rand Afrikaans University, Johannesburg, using HPLC for nectar chemistry.

INSECT OBSERVATION, POLLINATION MECHANISMS AND POLLEN LOAD ANALYSIS

Observations of insects visiting *Moraea* flowers included 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. To prevent contamination of the body of an insect with pollen carried by another in the same jar, each insect was wrapped in a paper tissue as soon as it was immobilized by jar fumes. Body length and proboscis length of insects were recorded. Pollen was removed from insects after specimens were pinned. Removal of pollen from insect bodies involved noting where pollen grains were located and gently scraping pollen from different parts of the body, including the scopae or corbiculae of bees, with a dissecting needle (see GOLDBLATT *et al.* 1998a, b, 2000a, b). The residue from needle probes was collected on glass slides and mounted in 1–2 drops of CALBERLA's fluid (OGDEN *et al.* 1974). Pollen grains were identified under white light microscopy by comparison with a set of pollen grain preparations made from co-blooming plants at study sites. *Moraea* pollen grains are recognized by their large size, reticulate exine, and single broad aperture. Some *Moraea* species, e.g.,

TABLE 1. — Study sites and voucher information for *Moraea* species for which we have original observations. Vouchers are housed at MO (GOLDBLATT & MANNING) or at NBG (other collectors). All study sites are in South Africa. Voucher information for additional species included in Table 4 may be found in GOLDBLATT *et al.* (1998b) and GOLDBLATT & BERNHARDT (1999).

Species		Study site	Voucher
<i>M. algoensis</i> Goldblatt	site 1	Eastern Cape, near Joubertina	Goldblatt & Porter 12362
	site 2	Western Cape, Kammanassie Mts	Goldblatt & Porter 12288
<i>M. angusta</i> (L.f.) Ker Gawl.		Western Cape, Sir Lowry's Pass	Goldblatt 11599
<i>M. australis</i> (Goldblatt) Goldblatt		Eastern Cape, Cape St Francis	Goldblatt & Porter 12351
<i>M. bifida</i> L. Bolus		Northern Cape, Glenlyon, Nieuwoudtville	Goldblatt 3969
<i>M. bipartita</i> L. Bolus		Western Cape, Seweweekspoort	Goldblatt & Porter 12331A
<i>M. brachygynae</i> L. Bolus		Western Cape, Kobee Pass	Goldblatt & Porter 11806
<i>M. brevistyla</i> (Goldblatt) Goldblatt		Free State, The Sentinel	Goldblatt & Manning 9859
<i>M. bulbifera</i> (G. J. Lewis) Goldblatt		Western Cape, Cloete's Pass	Goldblatt & Porter 12377
<i>M. calcicola</i> Goldblatt		Western Cape, Paternoster	Goldblatt & Manning 11134
<i>M. cantharophila</i> Goldblatt & J. C. Manning		Western Cape, Sandy's Glen	Goldblatt & Manning 11542
<i>M. aff. Cantharophila</i>	site 1	Western Cape, Groenland Mts	Goldblatt 11623
	site 2	Western Cape, Elgin	Goldblatt 11640
<i>M. ciliata</i> (L.f.) Ker Gawl.		Northern Cape, Bokkeveld Mts	Goldblatt s.n. no voucher
<i>M. cookii</i> L. Bolus	site 1	Western Cape, Pietermeintjies	Goldblatt & Nänni 11183
	site 2	Western Cape, Cold Bokkeveld	Goldblatt 11628
<i>M. demissa</i> Goldblatt		Western Cape, Gifberg plateau	Goldblatt & Manning 10963
<i>M. falcifolia</i> Klatt		Northern Cape, near Springbok	Goldblatt 9895
<i>M. fugacissima</i> (L.f.) Goldblatt		Western Cape, Wolseley	Goldblatt s.n. no voucher
<i>M. fugax</i> subsp. <i>diphylla</i> Goldblatt		Western Cape, N of Vanrhynsdorp	Manning s.n. no voucher
<i>M. fugax</i> (Delaroche) Ker Gawl. subsp. <i>fugax</i>		Western Cape, near Aurora	Goldblatt & Porter 11884
<i>M. gawleri</i> Spreng.	site 1	Western Cape, near Tulbagh	Goldblatt 11419
	site 2	Western Cape, Brandvlei hills	Goldblatt & Porter 12206
<i>M. inclinata</i> Goldblatt		Free State, Witzieshoek	Goldblatt & Nänni 11226
<i>M. inconspicua</i> Goldblatt		Northern Cape, Spektakel Pass	Goldblatt & Manning 9714
<i>M. insolens</i> Goldblatt		Western Cape, W of Caledon	Goldblatt & Porter 11832
<i>M. longistyla</i> (Goldblatt) Goldblatt		Western Cape, Burger's Pass	Goldblatt 4181
<i>M. lurida</i> Ker Gawl.	site 1	Western Cape, near Caledon	Goldblatt 11938
	site 2	Western Cape, near Botrivier	Goldblatt & Manning 11179
<i>M. marlothii</i> (L. Bolus) Goldblatt		Northern Cape, near Calvinia	Goldblatt Manning 10355A
<i>M. miniata</i> Andr.		Western Cape, near Citrusdal	Goldblatt 3928
<i>M. minor</i> (Eckl.) Goldblatt		Western Cape, near Hopefield	Goldblatt & Manning 11418
<i>M. papilionacea</i> (L.f.) Ker Gawl.		Western Cape, near Darling	Goldblatt s.n. no voucher
<i>M. polyanthos</i> Thunb.	site 1	Western Cape, near MacGregor	Goldblatt & Porter 12208
	site 2	Western Cape, near Oudtshoorn	Goldblatt & Porter 12277
	site 3	Western Cape, Calitzdorp	Goldblatt & Porter 12337
<i>M. pritzeliana</i> Diels		Northern Cape, Glenlyon, Nieuwoudtville	Goldblatt & Porter s.n. no voucher
<i>M. serpentina</i> Baker		Western Cape, near Vanrhynsdorp	Goldblatt 3075A
<i>M. speciosa</i> L. Bolus		Western Cape, Tanqua Karoo	Snijman 125
<i>M. tricuspidata</i> (D. Delaroche) Ker Gawl.		Western Cape, near Humansdorp	Goldblatt & Porter 12350
<i>M. trifida</i> R. C. Foster		Free State, The Sentinel	Goldblatt & Manning 11052
<i>M. tripetala</i> (L.f.) Ker Gawl.	site 1	Northern Cape, Nieuwoudtville	Goldblatt 3098
	site 2	Western Cape, Gifberg plateau	Goldblatt & Manning 10982
	site 3	Western Cape, Pakhuis Pass	Goldblatt & Manning 9631
<i>M. tulbaghensis</i> L. Bolus		Western Cape, near Moorreesburg	Goldblatt & Manning 11137
<i>M. unguiculata</i> Ker Gawl.		Western Cape, near Mossel Bay	Goldblatt & Porter 12372
<i>M. villosa</i> (Ker Gawl.) Ker Gawl.	site 1	Western Cape, Malmesbury	Goldblatt & Manning 6275
	site 2	Western Cape, near Tulbagh	Goldblatt 11420

M. collina Thunb., also have exine granules scattered over the apertural membrane.

Insect specimens were identified by R.W. BROOKS and C. MICHENER, University of Kansas

(Apoidea except Melittidae), H. DOMBROW, Worms, Germany (Scarabaeidae), KIM E. STEINER, California Academy of Sciences (melittid bees, Scarabaeidae), and D. BARACLOUGH,

Natal Museum (Diptera). Voucher specimens are deposited at the Natal Museum, Pietermaritzburg, South Africa or the Snow Entomological Museum, Lawrence, Kansas.

RESULTS

COMPARATIVE PHENOLOGY, MORPHOLOGY AND FLORAL PRESENTATION

Vegetative and floral morphology

Species of *Moraea* are seasonal geophytes, with an underground corm. With few exceptions, plants flower in the late winter and spring in the southern African winter-rainfall zone, or in the late spring and summer in the summer-rainfall zone (Table 2). Most species have living foliage leaves at flowering time, but a few that flower in the dry season have dry foliage leaves when in bloom (e.g., *M. pseudospicata*). In these species leaf production and vegetative growth occur during the wet season but flowering stems, inflorescences, and flowers are produced either in summer for the winter-rainfall zone, or early spring for the summer-rainfall zone. Vegetatively, *Moraea* species are surprisingly uniform, all sharing three derived features: a cormous rootstock composed of a single internode; corm tunics of conspicuous, persistent fibers; and a bifacial dorsiventral (rarely centric) leaf blade without a midrib, thus unlike the isobilateral, unifacial leaf of most other Iridaceae (GOLDBLATT 1986, 2001).

Flowers are borne in a specialized inflorescence, a rhipidium, which is a laterally compressed monochasial umbellate cyme with a contracted floral axis (GOLDBLATT 1990, 1991). The flower buds are enclosed within a pair of large, leafy, opposed bracts usually called spathes, and are raised sequentially above the spathes on slender pedicels the day before anthesis. Flowers are either fugaceous, evidently the ancestral condition (GOLDBLATT *et al.* 2002a), lasting only part of one day, and deliquescing on fading, or they last two or three days. Flowering in populations is closely synchronized in species with fugaceous flowers, thus over a large part of the range of a species, plants do not produce flowers on some days while on other days most individuals with

flowering stems produce one or more blooms. Opening and fading of fugaceous flowers is also synchronous and characteristic for a particular species (GOLDBLATT 1986; GOLDBLATT & BERNHARDT 1999). Floral longevity is associated with taxonomic affiliation and not with a particular pollination system (taxonomy following GOLDBLATT 1986, 1998). For example, species of subgenera *Grandiflora* and *Vieusseuxia* produce flowers that usually last three days. In contrast, flowers of most species of the *Homeria* group are fugaceous but a few last two days, e.g., *M. collina*, *M. ochroleuca*. Members of other infraspecific groups have fugaceous flowers.

Protandry, herkogamy and compatibility relationships

In all species the anthers dehisce shortly after the tepals expand, and pollen remains in the anther locules until disturbed by an insect visitor. We have no information on stigma receptivity but stigmatic lobes, which are appressed to style branch tissue in the bud, do not unfold and become available for pollen deposition until at least two to three hours after the tepals expand and anthers dehisce in short-lived fugaceous flowers (GOLDBLATT & BERNHARDT 1999). In species with long-lived flowers, the stigmatic lobes only unfold on the second day of anthesis. This pattern indicates partial mechanical protandry.

In addition to partial protandry, in the majority of species of *Moraea* the anthers and pollen are spatially separated from the stigmas, the latter held a short distance above the anther apices, sometimes up to 4 mm above them (Fig. 1B). Deposition of self pollen on the stigmas is not possible without some external agent. Moreover, most species of the genus studied for compatibility relationships have been found to be self-incompatible (GOLDBLATT 1981, 1987, and unpubl. data). In a limited number of species, most of them having the *M. miniata* type flower (see below) the anthers and stigmatic surfaces are in direct contact. Most of these species also exhibit complete self-incompatibility (GOLDBLATT 1981). However, observations have shown that at least one population each of *M. britteniae* (L. Bolus) Goldblatt, *M. collina*, *M. marlothii*,

and several populations of *M. albiflora* (G.J.Lewis) Goldblatt, *M. demissa*, *M. flavescens* Goldblatt, *M. longifolia* (Jacq.) Pers., *M. minor*, *M. pallida* Baker, and *M. vegeta* L. undergo successful mechanical self-pollination (autogamy) in the absence of floral foragers. Only *M. demissa* and *M. flavescens* are immediately related, but most of these species share certain features. In addition to direct spatial contact of anthers with stigmatic surfaces during anthesis, these features usually include a pale or dull-colored, white to dingy yellow to brownish perianth with indistinct nectar guides or other marks, absence of discernible floral odor, and smaller flowers than their immediate allies, which usually have scented flowers. When these plants bloom in a study greenhouse in the absence of floral foragers they set capsules after the anthers dehisce and pollen is shed directly onto the stigmas. The known self-compatible species belong to three of the five different flower types in the genus and are discussed below under those headings.

THE FIVE MAJOR TYPES OF FLORAL PRESENTATION AND THEIR POLLINATION TYPES (TABLE 2)

Based on perianth shape, pigmentation, scent and nectar, and associated suites of pollinators we recognize five major floral types in *Moraea* (Figs 1-4).

1. The *Iris*- (or *meranthium*-) type (Fig. 1)

Of the five significantly different flower types that we recognize in *Moraea*, the typical flower, shared by the majority of species may be characterized as the *Iris*-type (Fig. 1A-C). Such flowers comprise three large outer tepals, each with an ascending claw and a spreading to lightly reflexed limb (Fig. 1A, C). The claw lies facing one of the three style branches with its apex arching toward to apex of the style branch, above which extend the petaloid style crests. The three inner tepals are obscurely clawed and may be erect, have spreading limbs, or they may be reduced in size and have inconspicuous limbs or lack limbs completely. The filaments are united in the lower half and thus enclose the style; both free, distal parts of the filaments and the anthers are appressed to the abaxial surfaces of the style branches. The stigma consists of a transverse lobe of tissue on

the abaxial surface of the style branch lying just below the base of the paired petaloid crests and in most species above the anther apices.

A nectar gland is located at the base of each outer tepal claw (Fig. 1A, arrow). Each of the three outer tepal-style branch-crest pairs loosely resembles a single, bilabiate gullet flower and functions in pollination as a single unit (GOLDBLATT *et al.* 1989) exactly as has been described for *Iris*. Thus the flowers of *Iris* and *Moraea* have been described as meranthia in which a single flower functions as three separate floral units (MÜLLER 1883; KNUTH 1909; PROCTOR *et al.* 1996). Essentially they form bilabiate gullet flowers, broadly resembling those in many Lamiaceae and Scrophulariaceae, except that in *Moraea* the outer tepal limb forms the lower lip and the erect style crests the upper lip. The main difference between the flowers of *Iris* and *Moraea* is that in *Iris* the tepals are basally united and fused with staminal tissue to form a hypanthium tube, and nectaries are found in the interior walls of the hypanthium. In contrast, the tepals in *Moraea* are typically free, the filaments are partially to entirely united, and the nectary lies on the outer tepal claw.

The flowers are often scented but some species evidently lack floral odor. Floral odors are often sweet with a spicy element of cinnamon, clove, or vanilla (e.g., *Moraea ciliata*, *M. fugax*, *M. gracilentia* Goldblatt). Perianth colors are most often blue to blue-mauve or yellow, less often white (*M. brevistyla*, populations of *M. fugax* and *M. serpentina*) or pink to brick-red (*M. carnea* Goldblatt, some populations of *M. papilionacea*, *M. tricolor* Andr.). The tepal limbs bear a yellow to orange or white nectar guide at the base, often edged with darker color.

Within these species flower size ranges from relatively small in species like *Moraea gawleri* and *M. inclinata* (e.g., Fig. 1A, C) (outer tepals 16-28 mm long; limbs 9-16 mm long, claws 7-12 mm long) to quite large in species of subgenera *Monocephalae* and *Grandiflora* (outer tepals mostly 40-50 mm long; limbs 25-30 mm long, claws 15-20 mm long) (e.g., Fig. 1B). Thus, each of the three meranthia (or floral units) may have a gullet (the length of the tepal claw) as short as 7 mm to as long as 20 mm (the tepal

TABLE 2. — Floral characteristics of *Moraea* species arranged according to flower type. +, presence; –, absence.

Species	Flower shape	Dominant flower color	Location of tepal marks	Scent	Nectar	Flowering time
<i>Iris-type</i>						
<i>M. algoensis</i>	small iris	violet	outer tepals	no	+	Aug.-Oct.
<i>M. angusta</i>	large iris	yellow	outer tepals	no	+	Aug.-Sept.
<i>M. australis</i>	small iris	blue	outer tepals	yes	?	Sept.-Oct.
<i>M. bipartita</i>	small iris	blue	outer tepals	yes	+	Sept.-Oct.
<i>M. brevistyla</i>	small iris	white	outer tepals	no	+	Jan.-Feb.
<i>M. ciliata</i>	large iris	blue	outer tepals	yes	+	July-Aug.
<i>M. falcifolia</i>	small iris	white	outer tepals	no	+	July-Aug.
<i>M. fugax</i> subsp. <i>fugax</i>	large iris	yellow, blue, or white	outer tepals	yes	+	Aug.-Sept.
<i>M. fugax</i> subsp. <i>diphylla</i>	small iris	white	outer tepals	yes	+	Aug.-Sept.
<i>M. gawleri</i>	small iris	yellow	outer tepals	no	+	Aug.-Sept.
<i>M. inclinata</i>	small iris	blue	outer tepals	no	+	Aug.-Sept.
<i>M. inconspicua</i>	small iris	dull yellow	outer tepals	yes	+	Sept.
<i>M. papilionacea</i>	small iris	yellow or salmon	outer tepals	no	+	Aug.-Sept.
<i>M. pritzeliana</i>	small iris	blue	outer tepals	no	+	Aug.-Sept.
<i>M. serpentina</i>	small iris	white	outer tepals	no	+	Aug.-Sept.
<i>M. tricuspidata</i>	small iris	white	outer tepals	yes	+	Sept.-Nov.
<i>M. trifida</i>	small iris	pale yellow	outer tepals	no	+	Dec.-Feb.
<i>M. tripetala</i>	small iris	blue	outer tepals	no	+	July-Sept.
<i>M. unguiculata</i>	small iris	cream	outer tepals	no	+	Sept.-Oct.
<i>Moraea collina-type</i>						
<i>M. bulbifera</i>	cup	yellow	none	yes	+	Sept.-Oct.
<i>M. collina</i>	cup	pink or yellow	all tepals	yes	+	Aug.-Sept.
<i>M. fugacissima</i>	cup	yellow	none	yes	–	July-Aug.
<i>M. longistyla</i>	cup	pink or yellow	all tepals	no	+	Aug.-Sept.
<i>M. minor</i>	cup	pink	all tepals	yes	+	July-Aug.
<i>M. polyanthos</i>	cup	blue	all tepals	no	+	Sept.-Oct.
<i>M. vallisbelli</i>	cup	pink or yellow	all tepals	no	+	Aug.-Sept.
<i>Moraea miniata-type</i>						
<i>M. bifida</i>	star	pink or yellow	all tepals	yes	+	Aug.-Sept.
<i>M. cookii</i>	star	yellow	all tepals	yes	+	Sept.-Oct.
<i>M. lewisiae</i>	star	yellow	all tepals	yes	+	Sept.-Oct.
<i>M. longifolia</i>	star	dull yellow	none	no	?	Oct.
<i>M. miniata</i>	star	pink or yellow	all tepals	yes	+	Aug.-Sept.
<i>M. pseudospicata</i>	star	blue	all tepals	yes	+	July-Aug.
<i>M. reflexa</i>	star	yellow	all tepals	?	+	Oct.
<i>Moraea villosa-type</i>						
<i>M. bellendenii</i>	salver	yellow	outer tepals	no	?	
<i>M. calcicola</i>	salver	blue	outer tepals	no	–	
<i>M. cantharophila</i>	salver	cream	outer tepals	no	–	Sept.
<i>M. comptonii</i>	shallow bowl	yellow or pink with yellow bowl	all tepals	yes	+	July-Aug.
<i>M. elegans</i>	shallow bowl	yellow with green/orange marks	all tepals	yes	+	Aug.-Sept.
<i>M. insolens</i>	salver	orange	all tepals	no	–	Sept.
<i>M. tulbaghensis</i>	salver	orange	outer tepals	no	–	July-Aug.
<i>M. villosa</i>	salver	purple	outer tepals	no	–	Aug.-Sept.
<i>Moraea ochroleuca-type</i>						
<i>M. lurida</i>	bowl	usually maroon	none	yes	+	Aug.-Sept.
<i>M. ochroleuca</i>	bowl	yellow, or orange in bowl	none	yes	+	July-Aug.

claw is as long as the gullet). The tepals are fairly flexible and small and medium sized bees, can successfully squeeze their bodies into the gullets of smaller flowers while medium-sized to large bees effectively utilize larger flowers.

The inner tepals of flowers with the meranthium mode of presentation are usually somewhat smaller than the outer, and in many species of subgenus *Vieusseuxia* the inner tepals may have the limb reduced in size and either tricuspidate (e.g., *Moraea algoensis*, *M. brevistyla*, *M. trifida*) (Fig. 1D, F), or the entire tepal may be represented by a tiny cusp (*M. tripetala*) (Fig. 1E). Although to the human eye such flowers have a very different appearance, our observations, detailed below, show that their pollination biology is the same as more conventional *Moraea*-type flowers and for convenience we treat them together. The role of the inner tepals in floral display is thus uncertain and the success of species like the widespread and common *M. tripetala* that lack inner tepals suggests that they play at best a limited role in floral attraction.

Provisionally, the flowers of *Moraea inconspicua* and a variant of *M. unguiculata* that has brownish tepals are included in this group. The flowers are small, with outer tepals 13–16 mm long, the cream to yellow claws form a shallow cup and the brown tepal limbs, 9–12 mm long, are reflexed, thus directed downward. As a result, the short filament column and style branches are prominently displayed and the pollen and nectar are readily accessible to visiting insects. The flowers of *M. inconspicua* open relatively late in the afternoon and wilt after sunset whereas those of *M. unguiculata* remain fresh for two full days and wilt on the third. The only visitors to the flowers of *M. inconspicua* that we have recorded are potter wasps (see below).

Another variant of the *Iris*-type (meranthium) flower is represented by the few species in which the tepals are white or pale bluish to the human eye, lack prominent markings but are richly scented (e.g., *M. gracilentia*, *M. vespertina* Goldblatt & J.C.Manning, and *M. viscaria* (L.f.) Ker Gawl.). In flowers of this group, the perianth expands in the mid- to late afternoon (after 16:00H) and wilts shortly after twilight (GOLDBLATT 1986; GOLDBLATT & MANNING

2000). Unfortunately we have no pollinator observations for this flower type, which could be interpreted as adapted for moth pollination.

One species with flowers of the *Iris*-type, *Moraea vegeta*, is self-compatible and under laboratory and greenhouse conditions, autogamous. The flowers of this species are somewhat smaller and dull-colored compared to other species in this pollination group. No insect visitors have been recorded on flowers of this plant.

II. The *Moraea collina*- or *Homeria*-type (Figs 2A; 4C)

Most species with this type of floral presentation were included in the past in the genera *Galaxia* and *Homeria*. Functioning not as a meranthium but as a single unit, the *Homeria* flower type consists of a perianth with subequal tepals of similar disposition, size, shape, and color. The tepals of both whorls bear nectar guides and both usually have basal nectaries. In species of the *Galaxia* group, however, plants are acaulescent and the tepals are united into a solid tube that raises the flower above the leaves. These flowers lack nectaries, and do not produce nectar. Nectar guides are also absent. Most important, in this type of flower the tepal claws collectively form a narrow to wide cup surrounding a staminal column in which the filaments are fully united or free only apically. The style branches are much reduced in size and are about as wide or narrower than the anthers. As in the *Iris*-type flower, the anthers are appressed to the style branches. Distinctive, relatively sweet floral odors are often produced. Most flowers of this type are fugaceous, lasting just a single day and deliquescing when fading.

The tepal limbs spread horizontally above the floral cup which partly or completely encloses the stamen-style branch column (androgynophore). The flowers are usually pale yellow or light salmon-pink (often both colors occur in different populations of the same species), or pale to mid blue (e.g., *M. polyanthos*, *M. speciosa*), or rarely white (races of *M. polyanthos*). Nectar guides, when present are often obscure, and consist of darker pigmentation, but sometimes there are just a few small dark spots; when the perianth is blue the markings are yellow to orange.

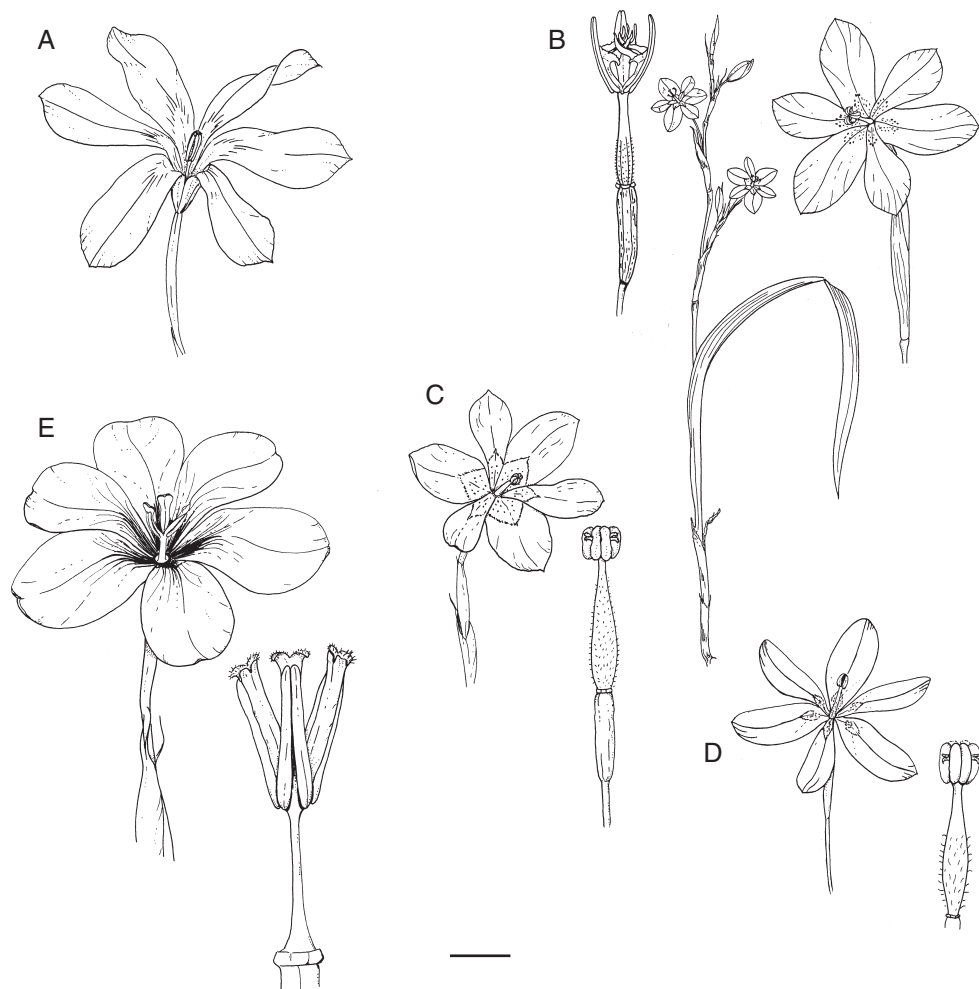


FIG. 2. — Bowl and salver type flowers in *Moraea*: **A**, the bowl-shaped flower of *M. collina*, with the style and stamens forming a column held within the floral cup; **B**, *M. marlothii*, showing entire plant, flower with columnar stamens and style branches, with enlarged detail of the androgynophore; **C**, **D**, rotate flowers of *M. bifida* (**C**) and *M. miniata* (**D**) with the androgynophore much enlarged; **E**, bowl-shaped flower of *M. ochroleuca*, showing the fly pollination syndrome, with the perianth lacking nectar guides and radiating veins that secrete nectar. Scale bar: 1 cm for flowers, floral dissections variously enlarged. Drawn by Margo BRANCH.

Flowers of a few species of the group, including *Moraea collina*, last into the second day of anthesis and then deliquesce. One population of *M. collina* studied, and several of *M. demissa* and *M. minor*, are self-compatible but as they have been observed to receive visits from pollinating insects, we consider them facultatively autogamous.

III. The *Moraea miniata*- or *stellate*-type (Figs 2B-D; 4D)

Flowers of the *Moraea miniata* type have tepals with short or obscure claws, 2-3(-4) mm long, that sometimes clasp the base of the filaments, thus forming a small cup, while the tepal limbs, mostly 14-20 mm, spread horizontally or may be reflexed (e.g., *M. reflexa* Goldblatt & J.C.Manning).

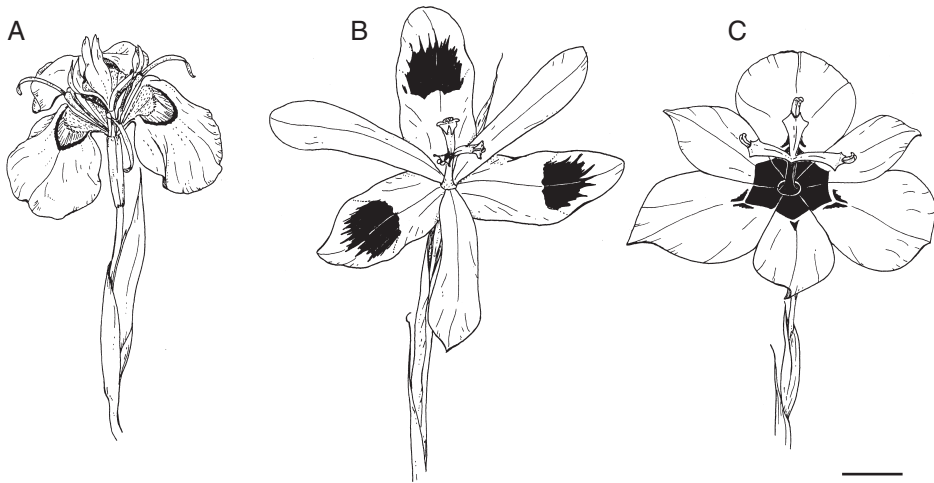


FIG. 3. — Beetle type flowers in *Moraea*, with examples from three different clades: **A**, *M. villosa*, with trilobed inner tepals and dark beetle marks the base of the outer tepals limbs; **B**, *M. elegans*, with salver shape and beetle marks on the outer tepals; **C**, *M. insolens*, with the base of the tepals and the filament column darkly colored. Note the salver shape in B and C. Scale bar: 1 cm. Drawn by Margo BRANCH.

More important, the filament column extends well above the tepal limbs so that the anthers and pollen are prominently displayed and are distant from the tepals. In many species with this flower type the anthers are erect and contiguous, thus concealing the style branches, the stigmatic tips of which may extend between the anthers when receptive.

In a variant of this flower (the *Hexaglottis* group of the genus), the style branches are fili-form and divided almost to the base, or less often are simple, and they extend more or less horizontally between the stamens (GOLDBLATT 1987). The divergent, relatively large anthers and their pollen are, nevertheless, prominently displayed.

Flowers of the *Moraea miniata*-type are typically fugaceous, reflecting their relationship to either the *Galaxia*, *Homeria* or *M. polyanthos* lineages of the genus and open and wilt at set times the same day that they open. Flowers typically open in early afternoon, but in some species, including *Moraea pseudospicata* Goldblatt and its ally, *M. crispa* Thunb., and those of the *Hexaglottis* group (GOLDBLATT 1987), flowers open in the later afternoon, after 16:00H, and fade at sunset. *Moraea worcesterensis* Goldblatt, for which we have no pollinator observations, has

flowers of the *M. miniata*-type, but it is a member of subgenus *Vieusseuxia* and flowers last three days.

One species with flowers of this group, *Moraea longifolia*, is autogamous under greenhouse conditions. In the field we noted that the flowers lack both scent and nectar guides, present in its close ally, *M. lewisiae* (Goldblatt) Goldblatt, which flowered at the same time as *M. longifolia* at our study site. *Apis* workers actively foraged for pollen on flowers of *M. lewisiae* but consistently ignored those of *M. longifolia*.

IV. The painted bowl (sensu BERNHARDT 2000) or *Moraea villosa*-type (Fig. 3)

Species with the painted bowl mode of floral presentation, of which *Moraea villosa* (Figs 3A; 4B) is the most common example, may have well developed style branches and prominent crests, but each outer tepal and the opposed style branch do not function as separate units or mer-anthia. Instead, the outer tepals have short ascending claws and broadly ovate to round, overlapping limbs, 20–28 × 22–30 mm. The tepals extend horizontally forming a plane surface 50–60 mm in diameter. In most species with this flower type the inner tepals play little if any role in floral attraction. Reduced in size, they

have a short claw and tricuspidate limb, the central lobe of which is longest and more or less trails below the platform formed by the outer tepals (Fig. 3A).

Floral pigmentation is unusually vivid as the outer tepals have prominent and contrasting, blackish, navy blue, emerald green, or iridescent markings, the so-called “beetle marks”, often surrounding a central pale “eye” and equally pale tepal claws. Colors include deep purple or dark blue or bright orange with blackish to navy blue markings (*Moraea gigandra* L.Bolus, *M. loubseri* Goldblatt, *M. tulbaghensis*, *M. villosa*). Other patterns include cream with orange markings (*M. cantharophila*), or scarlet or pale green with a dark brown, patterned center (*M. insolens*) (Fig. 3C).

Flowers of *Moraea elegans* Jacq. and *M. comptonii* (L.Bolus) Goldblatt do not fall exactly within this group, largely because the flowers are strongly scented. The perianth forms a wide, shallow bowl or salver *c.* 55–80 mm in diameter, the filament column is held partly within the bowl, while the style branches, which arch over the anthers, are held above the bowl. The perianth in these two species is predominantly yellow or salmon-pink, but the tepals have bold markings, in *M. elegans* the limbs have large dark green and orange blotches (Fig. 3B), while the tepal claws of *M. comptonii* usually bear large green marks. Floral scent is a strong, sweet fruity odor resembling a combination of banana, coconut, and pineapple. Traces of nectar are secreted from nectaries at the base of the tepals. Some species of the *Galaxia* group of *Moraea* may also belong in the painted bowl flower group, e.g., *M. barnardiella* Goldblatt and *M. melanops* Goldblatt & J.C.Manning. Both have salver- to shallow bowl-shaped pink flowers with a dark purple-black center.

As in flowers of the other groups, the phenology of painted bowl type flowers reflects their phylogenetic relationships. *Moraea villosa* and its immediate allies, as well as *M. cantharophila* and *M. insolens*, belong to subgenus *Vieusseuxia*, and their flowers last three days. In contrast, *M. comptonii* and *M. elegans* belong to the *Homeria* group and their flowers are relatively short-lived, fading and deliquescent on the second day after anthesis.

V. The *Moraea ochroleuca*-type (Fig. 2E)

In just two species the perianth forms a relatively wide, deep bowl-shape, *c.* 20 mm wide, with the spreading tepal limbs, 12–17 mm long forming a rim around the bowl. The bowl formed by the tepal claws is about 12 mm at the deepest, and partly includes the androgynophore. The flowers produce a strong putrid odor of rotting flesh. The flowers most closely resemble those of the *M. collina*-type but in *M. ochroleuca* (Salisb.) Drapiez the bowl is wider, and nectar is secreted from prominent veins over the surface of the tepal claws, rather than from discrete nectaries, and there is the obvious difference in floral odors. Colors are yellow to orange in *M. ochroleuca* or dark livery maroon (sometimes feathered with pale yellow or cream) in *M. lurida* but obvious nectar guides are lacking.

Reflecting their taxonomic affiliation, the flowers of *Moraea ochroleuca* (which is closely related to *M. collina*) are short lived, fading and deliquescent on the second day after anthesis while those of *M. lurida* (which belongs to subgenus *Vieusseuxia*) last three days.

NECTAR

With the exception of species with the painted bowl type flower, *Moraea* species produce small quantities of nectar, even when pollen is the major reward. In most species nectaries are visible as small discrete, shiny zones close to the base of the outer or both whorls of tepals. In flowers of the meranthium- or *Iris*-type, nectaries are present only on the outer tepal claws. In other flower types nectaries are present on all six tepal claws, but the nectar glands are usually smaller on the inner tepals. *Moraea lurida* and *M. ochroleuca* are exceptions (see above) as nectar secretion is restricted to the veins that run along the adaxial (upper) surface of the tepal claws.

In all species so far examined, nectar volumes are small and rarely sufficient to measure for volume. Some species appear to be nectarless under field conditions but usually applying the tongue to the nectaries yields a trace of sweetness. Volumes can be optimized if flowers are bagged or buds on cut stems are allowed to open in the laboratory. Painted bowl type flowers, e.g., *M. cantharophila*, *M. tulbaghensis*, *M. villosa*, etc.,

TABLE 3. — Nectar characteristics of species studied. Nectar chemistry analyses were provided by B.-E. VAN WYK, Rand Afrikaans University, Johannesburg. Data for *M. bifida*, *M. collina*, *M. reflexa*, and *M. ochroleuca* are from GOLDBLATT & BERNHARDT (1999).

Species	Nectar		Fru	Sugar ratios %			Ratio sucrose Fru + Glu (n)
	volume µl (n)	conc. % (± SD)		Glu	Suc		
<i>M. algoensis</i>	0.5 (5)	> 50%	n/a	n/a	n/a	n/a	
<i>M. bifida</i>	< 0.5 (5)	> 50%	50-51	49-50	0	0 (2)	
<i>M. bipartita</i>	< 0.5 (5)	> 50%	n/a	n/a	n/a	n/a	
<i>M. brevistyla</i>	0.2 (2)	> 50%	n/a	n/a	n/a	n/a	
<i>M. collina</i>	0.2-0.6 (4)	47.8 (2.1)	47-52	48-53	0	0 (4)	
<i>M. cookii</i>	n/a	n/a	53	47	0	0 (1)	
<i>M. huttonii</i>	< 0.5 (5)	> 50%	49	49	2	0.02 (1)	
<i>M. incurva</i>	< 0.5 (3)	> 50%	56	41	3	0.03 (1)	
<i>M. marlothii</i>	0.5-0.7 (2)	> 50%	48	49-52	0-3	0.02 (2)	
<i>M. ochroleuca</i>	< 0.5 (5)	> 50%	49-50	50-51	0	0 (2)	
<i>M. polyanthos</i>	< 0.5 (5)	> 50%	n/a	n/a	n/a	n/a	
<i>M. reflexa</i>	2.5-5.0 (2)	9.0-12.0	50.5	49.5	0	0 (2)	
<i>M. tricuspidata</i>	< 0.5 (5)	33-42	n/a	n/a	n/a	n/a	
<i>M. tripetala</i>	< 0.5 (5)	> 50%	56-57	43-44	0	0 (2)	

irrespective of taxonomic relationship remain nectarless under both field and laboratory conditions.

Nectar concentrations (Table 3) range from c. 12% sucrose equivalents in *M. reflexa* (GOLDBLATT & BERNHARDT 1999) to 47% in *M. collina*. In several species the concentration is greater than 50% and hence not measurable using a standard refractometer.

Nectar sugar analyses show consistently that *Moraea* nectar is hexose-dominant, with little or no sucrose present (Table 3). Hexose-rich or hexose-dominant nectar is uncommon in the insect pollinated Iridaceae of southern Africa but has been noted previously in four species of *Moraea* (GOLDBLATT & BERNHARDT 1999). Other genera, including *Babiana*, *Gladiolus*, *Hesperantha*, *Ixia*, *Lapeirousia*, and *Sparaxis*, all have sucrose-rich or sucrose-dominant nectar, except for a hexose-rich subset of species in which the flowers are pollinated by sunbirds or butterflies (GOLDBLATT *et al.* 1995, 1999, 2004; GOLDBLATT & MANNING 2002b). In these genera even flowers pollinated by sunbirds may be sucrose-rich, although some may be hexose-rich. Significantly, the above genera belong in subfamily Crocoideae (syn. Ixioidae) in which flowers have a perianth tube and nectar is secreted from septal nectaries. The occasional presence of hexose-rich nectar in the subfamily, notably in *Chasmanthe*, a few *Gladiolus* species, as well as in

Klattia and *Witsenia* of subfamily Nivenioideae, is assumed to be the result of pollinator selection (GOLDBLATT 1993; GOLDBLATT *et al.* 1999) by sunbirds or butterflies.

Thus, *Moraea* does not follow the correlation linking large-bodied bees, long-proboscid flies, and moths to sucrose-rich or sucrose-dominant nectar as in Crocoideae. Nectar secreted by the perigonal nectaries of *Moraea* is exposed to the atmosphere and the higher osmotic potential of hexose dominant nectar may be important under these conditions, preventing selection for higher sucrose levels. Similar levels of hexose-dominant nectar are characteristic of species of *Ferraria*, the sister genus of *Moraea*, which also has perigonal nectaries and a shallow bowl-shaped perianth (GOLDBLATT & MANNING unpubl. data).

KNOWN INSECT POLLINATION MECHANISMS AND POLLEN LOAD ANALYSES

The five major modes of floral presentation for insect pollination are accompanied by different suites of pollinators. Foragers to *Moraea* flowers have one characteristic in common. Field observations of flight and foraging patterns of insects coupled with analyses and identification of their pollen loads indicate that almost all *Moraea* insects also forage on the flowers of co-blooming plants for nectar and/or pollen (Table 4). The sapromyiophilous *M. lurida* and *M. ochroleuca*, are an apparent exception. There may not be

other suitable flowers available for the Diptera that visit these species and some captured flies have been found with pure loads of pollen of their hosts (Table 4).

I. The *Iris*- (or *meranthium*-) type

Smaller flowers of this group are visited by a range of small to medium-sized bees (body lengths 10–12 mm) as well as some halictid bees with smaller bodies, 5–7 mm long, that forage for nectar (Fig. 4A). Visitors range from one or two bee species at a particular site to as many as six (Table 4). Bees include members of five families: Apidae (*Amegilla*, *Anthophora*, *Apis*, *Xylocopa*); Halictidae (*Lasioglossum*, *Patellapis*), Colletidae (*Colletes*), Megachilidae (*Megachile*); and Melittidae (*Rediviva*). Thus, species with the *M. inclinata*-type may be pollinated by a combination of both long-tongued families, Apidae and Megachilidae and short-tongued families, Colletidae and Melittidae (GOLDBLATT *et al.* 1989).

Larger flowers of the group are visited primarily by large-bodied, hairy bee species, also foraging for nectar. Captured bees include *Amegilla capensis*, *A. spilostoma*, *Anthophora diversipes*, *A. krugeri*, *A. schulzei* (body lengths 13–16 mm and mouthparts 6–8 mm long) (Table 4), but we are confident that other large, long-tongued bees will also be found foraging on species of the group. We have also noted occasional visits to *Moraea* flowers by the common, large pierid butterflies, *Colias electo* and *Vanessa cardui*. These insects appear to be opportunistic foragers on nectar, but they are poor pollen vectors because only their probosces can contact anthers and stigmas while they feed because of the position of these organs relative to the foraging posture of butterflies. We wonder if they even succeed in feeding on concealed nectar given the usually high nectar concentration typical of *Moraea* species, usually more than 50% sucrose equivalents (Table 3). Nectar of this concentration is most likely too viscous to be sucked through their long, narrow probosces.

In the absence of observations of insect visitors for the three species listed above with white to pale blue *Iris*-type flowers that open after 16:00H, we hypothesize that they may be comparable to the white-flowered species of the genus

Hesperantha (Iridaceae) in which female bees and *Apis mellifera* workers have been recorded for evening blooming, white-flowered species of the genus *Hesperantha* (Iridaceae) (GOLDBLATT *et al.* 2004). The white-flowered species of this genus open in the late afternoon when they become scented and are visited by anthophorine bees and *Apis mellifera* until sunset, and then by a range of relatively small settling moths of several families, including the Drepanogynidae and Noctuidae. These crepuscular *Moraea* species need additional study, but we doubt that moths play an important role in their pollination because moths, like butterflies, are likely to be poor pollen vectors and in *Moraea* it is unlikely that small moths would contact the small, concealed anthers while taking nectar from the base of the tepals.

The pollination system in *Moraea inconspicua* and the variant of *M. unguiculata* that has dull yellow to brownish tepals is tentatively treated as a bee system but we note that the only visitors to the flowers of *M. inconspicua* that we have recorded are two unnamed species of potter wasp, *Tricaridinodynerus* sp. and *Parachilus* sp. (Vespidae). These wasps were the only visitors we noted on the flowers of the species but they did carry dorsal loads of pollen and could potentially deposit pollen on receptive stigmatic lobes. Their behavior is, as far as we can tell, much the same as bees foraging for nectar. Confirmation of wasp pollination is needed, particularly as this system would be novel not only for *Moraea* but for the southern African flora.

II. The *Moraea collina*-type

Narrow, cup-shaped flowers of this type are more likely to be generalist pollinated, receiving a range of pollen vectors including medium-sized bees, especially Halictidae, *Apis mellifera*, some hopliines, and occasionally muscid flies. These flowers are usually fairly sweet scented, a feature especially associated with pollination by bees. Insect collections and pollen load analyses show that fly visits may be relatively unimportant (GOLDBLATT & BERNHARDT 1999). In contrast, hopliine scarab beetles are encountered so frequently, and carry heavy loads of pollen, that they are evidently part of the legitimate spectrum of pollinators (Table 4).

TABLE 4. — Pollen load analysis of collected beetles, including original observations and data published by GOLDBLATT *et al.* (1998b) and GOLDBLATT & BERNHARDT (1989, 1999). Taxonomic affiliations of insects are as follows: Coleoptera: *Anisochelus*, *Anisonyx*, *Anisothrix*, *Argoplia*, *Heterochelus*, *Monochelus*, *Peritrichia*, *Platycheilus* (Scarabaeidae). Diptera: *Anthomyia* (Anthomyiidae); *Musca*, *Orthellia* (Muscidae); *Scathophaga* (Scathophagidae). Hymenoptera-Apoidea: *Andrena* (Andrenidae); *Allodapula*, *Amegilla*, *Anthophora*, *Apis* (Apidae); *Colletes* (Colletidae); *Lasioglossum*, *Nomia*, *Patellapis*, *Zonalictus* (Halictidae); *Afranthidium*, *Megachile* (Megachilidae); *Rediviva* (Melittidae); Hymenoptera-Vespoidea: *Parachilus*, *Tricarinydnerus* (Eumenidae). Asterisk (*) indicates more insects seen but not captured.

Plant and insect taxon			Number of insects carrying pollen loads of:		
			host flower only	host flower + other sp.	other sp. only or no pollen
I. The <i>Iris</i>- or meranthium-type					
<i>M. algoensis</i>	site 1	<i>Anthophora diversipes</i> ♀	0	2	0
		<i>Apis mellifera</i>	0	1	0
	site 2	<i>Amegilla spilostoma</i> ♀	0	3	1
<i>M. angusta</i>		<i>Anthophora diversipes</i> ♀	0	3	0
<i>M. australis</i>		<i>Apis mellifera</i> *	2	5	0
<i>M. bipartita</i>		<i>Apis mellifera</i> *	3	2	0
<i>M. brevistyla</i>		<i>Amegilla spilostoma</i>	0	2	0
From GOLDBLATT & BERNHARDT (1989)		<i>Lasioglossum</i> sp.	0	1	1
<i>M. ciliata</i>		<i>Anthophora diversipes</i> ♀	0	1	0
		<i>Anthophora schulzei</i> ♀	0	1	0
		<i>Anthophora krugeri</i> ♀	0	1	0
<i>M. falcifolia</i>		<i>Apis mellifera</i>	0	3	0
<i>M. fugax</i> subsp. <i>diphylla</i>		<i>Megachile</i> sp. ♀	0	1	0
<i>M. fugax</i> subsp. <i>fugax</i>		<i>Patellapis</i> aff. <i>schulzei</i> 3 ♀ ♀ 1 ♂	1	3	0
<i>M. gawleri</i>	site 1	<i>Apis mellifera</i> *	3	2	0
	site 2	<i>Rediviva peringueyi</i> ♀	0	1	0
		<i>Plesanthidium wolkmannii</i> ♀	0	1	0
	site 3	<i>Anthophora diversipes</i> ♀	0	2	0
		<i>Apis mellifera</i> *	0	5	0
<i>M. inclinata</i>		<i>Apis mellifera</i>	2	1	0
		<i>Amegilla capensis</i>	0	1	
From GOLDBLATT <i>et al.</i> (1989)		<i>Allodapula variegata</i> ♀	1	0	0
		<i>Amegilla africana</i> ♀	1	0	0
		<i>Amegilla capensis</i> ♀	0	1	0
		<i>Colletes</i> sp. ♀	0	0	0
		<i>Lasioglossum</i> spp. ♀	4	4	0
		<i>Nomia</i> spp. ♀	0	3	0
		<i>Megachile</i> sp. ♀	0	0	0
		<i>Zonalictus</i> sp. ♀	0	2	0
<i>M. inconspicua</i>		<i>Tricarinydnerus</i> sp. 1	0	1	0
		<i>Tricarinydnerus</i> sp. 2	0	1	0
		<i>Parachilus</i> sp.	0	1	0
<i>M. papilionacea</i>		<i>Rediviva peringueyi</i> ♀	0	2	0
<i>M. pritzeliana</i>		<i>Apis mellifera</i>	2	0	0
		<i>Rediviva macgregoriana</i> ♀	2	2	0
<i>M. serpentina</i>		<i>Apis mellifera</i>	2	0	0
<i>M. tricuspidata</i>		<i>Apis mellifera</i>	0	3	0
<i>M. tripetala</i>	site 1	<i>Apis mellifera</i>	0	2	0
		<i>Megachile johannis</i> 2 ♀	0	2	0
	site 2	<i>Apis mellifera</i>	1	3	0
	site 3	<i>Anthophora schulzei</i> 2 ♀	0	2	0
<i>M. unguiculata</i>		<i>Patellapis pearstonensis</i> ♀	0	2	0
		<i>Allodapula variegata</i> ♀	0	2	0

Plant and insect taxon			Number of insects carrying pollen loads of:		
			host flower only	host flower + other sp.	other sp. only or no pollen
II. The <i>M. collina</i>-type - flask (narrow cup) flowers					
<i>M. bulbifera</i>					
		<i>Megachile</i> sp. ♀	0	2	0
		unidentified hopliine	1	1	0
		unidentified hopliine	0	1	0
<i>M. collina</i> (GOLDBLATT & BERNHARDT 1999)					
		<i>Anisonyx ursus</i>	3	0	0
		<i>Apis mellifera</i>	0	4	0
		<i>Lasioglossum pearstonensis</i> ♀	0	0	7
		<i>Patellapis</i> sp. ♀	0	3	0
<i>M. longistyla</i>		<i>Anthophora diversipes</i> ♀	0	3	0
<i>M. minor</i>		<i>Lepisia rupicola</i>	3	2	0
		unidentified hopliine	0	3	0
<i>M. polyanthos</i>	site 1	<i>Anthophora</i> sp. ♀	0	1	0
		<i>Lasioglossum</i> sp. 3 ♀ ♀	1	2	0
	site 2	<i>Apis mellifera</i> *	2	2	0
	site 3	unidentified hopliine	1	0	0
<i>M. speciosa</i>		<i>Apis mellifera</i> *	4	1	0
<i>M. vallisbelli</i>	site 1	<i>Anthophora diversipes</i> ♀	0	1	0
	site 2 (GOLDBLATT <i>et al.</i> 1998b)	<i>Anisochelus inornatus</i>	6	5	2
III. The <i>M. miniata</i>-type - stellate flowers					
<i>M. bifida</i>	site 1	<i>Megachile johannis</i> ♀	0	1	0
	site 2	<i>Apis mellifera</i>	4	1	0
site 3 (GOLDBLATT & BERNHARDT 1999)		<i>Apis mellifera</i>	0	3	0
		<i>Rediviva macgregorii</i> ♀	0	2	0
<i>M. brachygyne</i>		<i>Apis mellifera</i>	2	2	0
		<i>Anthophora krugeri</i> ♀	0	2	0
<i>M. cookii</i>	site 1	<i>Anthophora schulzei</i> 1 ♀ 1 ♂	0	2	0
	site 2	<i>Amegilla fallax</i> ♀	0	1	0
		<i>Anthophora diversipes</i> * 4 ♀ ♀	0	4	0
		<i>Afranidium</i> sp. ♀	0	1	0
		<i>Xylocopa rufitarsis</i> * ♀	0	1	0
<i>M. demissa</i>		<i>Anthophora schulzei</i> ♀	0	1	0
		<i>A. diversipes</i> ♀	0	2	0
		<i>Rediviva longimanus</i> ♀	0	1	0
<i>M. lewisiae</i> (GOLDBLATT 1987)		<i>Apis mellifera</i> (numerous individuals, no pollen load analysis done)			
<i>M. marlothii</i>		<i>Andrena</i> sp. ♀	0	2	0
<i>M. miniata</i>		<i>Apis mellifera</i>	0	2	0
From GOLDBLATT & BERNHARDT (1999)		<i>Apis mellifera</i>	0	3	0
		<i>Rediviva parva</i> ♀	0	3	0
		<i>Rediviva longimanus</i> ♀	0	1	0
		<i>Anthophora diversipes</i> 3 ♀ ♀	0	3	0
<i>M. pseudospicata</i> (GOLDBLATT & BERNHARDT 1999)					
		<i>Apis mellifera</i>	5	2	0
		<i>Lasioglossum</i> sp. 3 ♀ ♀	1	1	1
<i>M. reflexa</i> (GOLDBLATT & BERNHARDT 1999)					
		<i>Apis mellifera</i>	2	0	0

Plant and insect taxon			Number of insects carrying pollen loads of:		
			host flower only	host flower + other sp.	other sp. only or no pollen
IV. <i>M. villosa</i>-type					
<i>M. bellendenii</i> (GOLDBLATT <i>et al.</i> 1998b)		<i>Heterochelus unguiculatus</i>	1	3	0
<i>M. calcicola</i>		<i>Pachychelus unguiculatus</i>	0	1	0
<i>M. cantharophila</i>	site 1	<i>Anisonyx</i> sp.	7	3	0
	site 2 (GOLDBLATT <i>et al.</i> 1998b, as <i>M. aff. lurida</i>)	<i>Peritrichia pseudoplebia</i>	0	6	0
		<i>Anisonyx ursus</i>	3	4	3
<i>M. aff. cantharophila</i>	site 1	<i>Anisonyx hessei</i>	8	0	0
	site 2	<i>Patellapis</i> sp. ♀	2	0	0
<i>M. comptonii</i> (GOLDBLATT <i>et al.</i> 1998b)		<i>Apis mellifera</i>	0	3	0
		<i>Anthophora diversipes</i> 2 ♀♀	0	2	0
		<i>Orthellia</i> sp.	5	0	0
		<i>Platychelus lupinus</i> (as <i>P.</i> sp.)	2	2	0
<i>M. elegans</i> (GOLDBLATT <i>et al.</i> 1998b)		<i>Apis mellifera</i>	2	0	0
		<i>Orthellia</i> sp.	0	2	1
		<i>Peritrichia pseudoplebia</i>	7	2	1
		<i>Scathophaga stercoraria</i>	0	0	3
<i>M. insolens</i> (GOLDBLATT <i>et al.</i> 1998b)		<i>Peritrichia pseudoplebia</i>	6	3	0
		<i>Dichelus expansus</i>	0	2	0
		<i>Anisonyx lepidotus</i>	1	1	0
<i>M. tulbaghensis</i>		<i>Apis mellifera</i>	0	2	0
		<i>Heterochelus detritus</i>	1	1	0
		<i>Argopia glaberrimus</i>	0	2	0
		<i>Monochelus steineri</i>	0	2	0
		<i>Anisochelus inornatus</i>	4	1	0
<i>M. villosa</i>	site 1	<i>Anisonyx ursus</i>	1	1	0
	site 2	<i>Leptocnemis steineri</i>	1	3	1
	site 3 (GOLDBLATT <i>et al.</i> 1998b)	<i>Anisonyx ditus</i> (as <i>A. longipes</i>)	1	6	0
		<i>Anisonyx ursus</i>	0	3	0
V. The <i>M. ochroleuca</i>-type - unmarked wide bowl flowers					
<i>M. lurida</i>	site 1	<i>Scathophaga stercoraria</i>	2	0	0
	site 2	<i>Orthellia</i> sp.	0	2	0
		<i>Musca</i> sp.	1	0	1
		<i>Scathophaga stercoraria</i>	2	0	0
<i>M. ochroleuca</i> (GOLDBLATT & BERNHARDT 1999)					
		<i>Anisonyx ursus</i>	2	0	0
		<i>Anthomyia</i>	0	0	1
		<i>Apis mellifera</i>	3	1	0
		Calliphoridae	0	0	1
		<i>Orthellia</i> sp.	10	0	0
		<i>Musca</i> sp.	0	2	1
		<i>Scathophaga stercoraria</i>	0	2	3
		Syrphidae	0	1	0
Total			131	210	28

The only pollinators thus far captured visiting the self-compatible *M. minor* are hopliine beetles, while hopliines are the most frequent visitors to the closely related *M. vallisbelli*. This supports the conclusion that hopliines are legitimate pollinators of some species of this group. They may then be considered to have a bimodal pollination system.

III. The *Moraea miniata*-type

Subject of a study by GOLDBLATT & BERNHARDT (1999), species with this flower type have their anthers borne on a prominent column held well above the spreading tepal limbs (Fig. 4D). Females and workers of four different bee families have been collected foraging for pollen in flowers of this type. The bee taxa include Apidae (*Amegilla*, *Anthophora*, *Apis*), Halictidae (*Lasioglossum*, *Patellapis*), Megachilidae (*Megachile*), and Melittidae (*Rediviva*) (Table 4). Bees appear to visit flowers primarily to collect pollen and typically land on the column, grasp the anthers between their legs and transfer the pollen to corbiculae or scopae. We discriminate between bee pollination in the *M. miniata*-type flower and bee pollination in the meranthium or *Iris*-type flower because of the strikingly different mode of floral presentation and the associated divergent behavior patterns of bees, either foraging for nectar and acquiring dorsal loads of pollen passively versus the active harvest of prominently displayed pollen. In *M. miniata*-type flowers bees occasionally probe the base of the tepals, presumably seeking nectar, a secondary activity compared to pollen collection. This mode of pollination converges with the many examples of nectarless, or near nectarless flowers offering copious pollen to female bees foraging for nest provisioning (BERNHARDT 1996).

IV. The painted bowl or *Moraea villosa*-type

As published elsewhere for species with this flower type the nectarless flowers are pollinated almost exclusively by hopliine scarab beetles (Scarabaeidae, Hopliini) (Fig. 4B). The salverform or shallow bowl perianth serves as a site for assembly, competitive behavior, mate selection, and copulation (STEINER 1998; GOLDBLATT &

MANNING 1996; GOLDBLATT *et al.* 1998b). As STEINER has shown for *M. villosa* and *M. tulbaghensis* (which now includes *M. neopavonia* R.C.Foster: GOLDBLATT & MANNING 2002a), medium-sized to large hopliines of several genera may visit the flowers of the same species with beetle density and diversity varying from season to season and locality to locality (Table 4). Our new observations for the relatively widespread *M. villosa* document for the first time visits by *Anisonyx* sp. 1 to flowers of populations near Tulbagh. Other hopliine pollinators of *M. villosa*, all from the Malmesbury district, include *Anisochelus inornatus*, *Anisonyx ditus*, *A. ursus*, *Lepithrix lebisii*, *L. ornatella*, and *Peritrichia rufotibialis* (STEINER 1998; GOLDBLATT *et al.* 1998b).

Observations published for *Moraea* aff. *lurida* (GOLDBLATT *et al.* 1998b) are now shown to represent the new species, *M. cantharophila* (GOLDBLATT & MANNING 2002a). This species is visited at Sir Lowry's Pass by *Anisonyx ursus* and *Peritrichia cinerea* and by *Anisonyx* sp. 2 at its other known station, Sandy's Glen (Table 4). *Moraea tulbaghensis* (including *M. neopavonia*), and *M. villosa* receive visits from the greatest number of hopliine species. For *M. tulbaghensis* these include *Lepithrix ornatella*, *Monochelis steineri*, and *Peritrichia abdominalis* at two sites (STEINER 1998) while in September 1998 and 1999 at another site we recorded *Anisochelus inornatus*, *Argoplia glaberrimus*, *Heterochelus detritus*, and *Monochelis steineri*, as well as *Apis* workers (Table 4).

Moraea comptonii and *M. elegans* may not strictly belong in this group for their strongly scented, shallow, bowl-shaped flowers are visited by a range of insects that usually includes some bees such as *Apis mellifera* and *Anthophora diversipes*, and occasionally muscid flies, as well as hopliine beetles (Table 2). The strong fruity scent is a feature more often associated with bee rather than fly or beetle pollination and the significance of fly visits is difficult to gauge. Hopliines and bees are encountered so frequently on these flowers they must be assumed to be part of the legitimate spectrum of pollinators of these large flowers, which have bold contrasting markings, as in *M. elegans*.

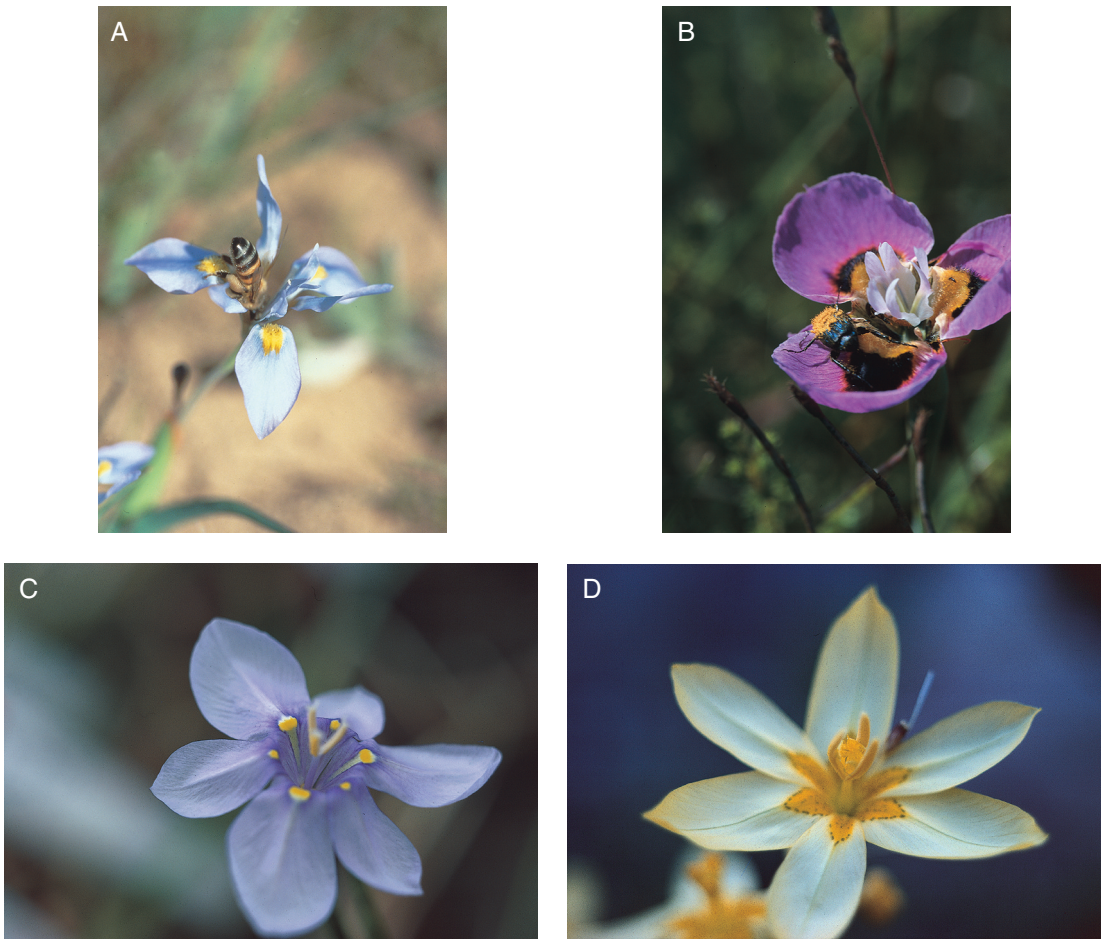


FIG. 4. — Flowers types in *Moraea* and some of their pollinators: **A**, *M. tripetala*, with an *Iris*-type flower, being visited by native *Apis mellifera*; **B**, *M. villosa*, showing prominent “beetle marks” and the black hopliine beetle, *Anisonyx ursus*, with heavy dorsal load of orange pollen; **C**, *M. polyanthos*, typical bowl type flower with stamens and style branches held within the deep floral cup; **D**, *M. marlothii*, a stellate type flower with stamens and style branches forming an androgynophore supporting anthers well above the flower.

Hopliine foraging has been described in detail by STEINER (1998) and GOLDBLATT *et al.* (1998a) and need not be repeated here. These beetles are now widely accepted as an important part of the pollinator spectrum in the southern African winter-rainfall zone. Hopliines are believed to play an important role in selection for particular floral traits including bright perianth color, contrasting markings, absence of nectar or floral odor, and a salverform shape (e.g., STEINER 1998; GOLDBLATT *et al.* 2000a, b).

V. The *Moraea ochroleuca*-type

These putrid smelling flowers are visited primarily by dung, game, and flesh flies in the families Calliphoridae, Muscidae, and Sarcophagidae. Occasional visits by other insects including hoverflies (Syrphidae), Anthomyidae, *Apis* workers, and even hopliine beetles have also been noted at some study sites (GOLDBLATT & BERNHARDT 1999) but these insects are probably no more than occasional visitors. At most sites where the fairly common *M. ochroleuca* is encountered only

the calliphorid, *Chrysomyia* sp. (body c. 9 mm long), diverse muscids, and sarcophagids are routinely seen on its flowers. *Moraea lurida*, the other species in this group, receives the same set of pollinators (Table 4). Flies always carry conspicuous dorsal loads of bright yellow or orange pollen, mainly on their thoraxes, acquired while crawling over the tepals as they take nectar from the diffuse nectaries. All of these flies have short mouth-parts and are usually associated with liquid diets, but not exclusively nectar.

Effective fly pollinators are relatively large, 7–11 mm long and stand 5–6 mm high. This brings the dorsal part of their thorax to the level of the anthers and receptive stigmatic lobes, which arch outward over the tepal cup, as they crawl over the tepal claw while foraging for nectar. Receptive stigma lobes thus readily receive loads of pollen as flies carrying dorsal loads of pollen move to flowers which are in female phase.

Self-compatible species

Of the several species that are known to be self-compatible, at least *Moraea minor* receives visits from hopliine beetles, while large female anthophorine bees have been captured foraging for pollen on the complex heterozygote, *M. demissa*. *Moraea collina* is regularly visited by bees and hopliines. In addition, hybrids have been recorded between *M. albiflora* and outcrossing *M. fugacissima* (GOLDBLATT 1979) which is pollinated by pollen-collecting bees, mainly *Apis* workers. This indicates that *M. albiflora* must, at least occasionally, receive visits from these bees, and visits by small bees to its flowers were noted by GOLDBLATT (1979). The self-pollinating species of *Moraea* are probably best regarded as facultatively autogamous members of one of the five pollination groups of *Moraea*, as defined by their floral presentation.

DISCUSSION

Although *Moraea* consists of some 195 species and shows broad interspecific variation in modes of floral presentation, information relating to its basic floral biology has been remarkably late and slow to accumulate. SCOTT-ELLIOT (1891) noted

a variety of insect visitors to several *Moraea* species, but while he did discriminate between casual visitors (ants stealing nectar) and others, he did not record which of these insects actually contacted the pollen-bearing anthers and stigma lobes. His observations are consequently of limited value. Particularly unsatisfactory are his sightings of the common hairy black hopliine, *Anisonyx ursus*, on flowers of species such the bee pollinated *M. angusta* and *M. fugax* (as *M. edulis* (L.f.) Ker Gawl.). Of the autogamous *M. vegeta* (as *M. tristis* L.) SCOTT-ELLIOT observed, “visitors very rare”, but as he noted none in his text we assume he saw no visitors to the species. We agree in general with his descriptions of *M. papilionacea* and *M. tripetala* as being pollinated by Apoidea and of *M. (Homeria) collina* and *M. (Homeria) elegans* as being pollinated by hopliines and bees although we believe the latter plant was probably *M. lewisiae* or *M. virgata* Jacq. (*M. elegans* does not occur naturally in Cape Town where he made his observations, nor does his description of the flower accord with that species).

VOGEL (1954) included *Moraea* in his monograph treating the pollination of many genera native to southern African and hypothesized that most species were pollinated by bees. His conclusion was evidently based primarily on observation of floral form and a review of the earlier literature rather than field observations of floral visitation. He hypothesized that the white, sweetly scented flowers of *M. viscaria* (syn. *M. odorata*), which open in the late afternoon, were pollinated by moths. Based on his reading of MARLOTH (1917), which has an illustration of *M. lurida*, he correctly interpreted its maroon, fetid-smelling flowers as fly-pollinated, while the *Iris*-like flowers of *M. tripetala* were inferred to be pollinated by butterflies, counter to SCOTT-ELLIOT’s (1891) conclusion.

Following SCOTT-ELLIOT’s preliminary observations, no work was done linking *Moraea* species with floral foragers until GOLDBLATT (1981) published the results of his studies on species of the *Homeria* group of *Moraea* (then treated as the separate genus, *Homeria*). He noted that cup- and bowl-shaped flowers (*M. collina*, *M. comp-tonii*, *M. ochroleuca*) were visited by Diptera with

sponging mouthparts whereas those with a stellate perianth and anthers and pollen prominently displayed on a filament column were visited by bees foraging primarily for pollen (*M. bifida*, *M. miniata*, *M. aspera* Goldblatt [syn. *Homeria spiralis* L.Bolus]). GOLDBLATT (1987) also described pollination by pollen collecting bees for the stellate, yellow, fragrant flowers of *M. lewisiae* and *M. virgata*, then included in the genus *Hexaglottis*. These flowers have prominently displayed anthers and attract female *Amegilla* sp. and native *Apis mellifera* workers that visit the flowers to forage primarily for pollen.

A brief paper by GOLDBLATT *et al.* (1989) compared the biomechanics of bee pollination in *Moraea inclinata*, and *M. brevistyla* to that in *Iris*. The authors noted that, as in the meranthia of *Iris* flowers, bees pollinating the two *Moraea* species must depress the lower tepal and are sandwiched between the tepal claw and the stamen-style branch complex while they forage for nectar. Successful foraging by bees emphasized enlarged body size and/or extended mouthparts even in "short-tongued" members of the family Halictidae. Similar conclusions were reached by PÉREZ CHISCANO (2001) who studied pollination in four populations of *M. sisyrinchium* (L.) Ker Gawl. in Spain. This author found that its moderate-sized *Iris*-like flowers were outcrossed and were pollinated primarily by *Apis mellifera*. His description of the foraging pattern exactly matches ours.

Although hopliine beetles have been associated with the consumption of pollen and nectar of many southern African plants since the late 19th and early 20th centuries (SCOTT-ELLIOT 1891; PERINGUEY 1902) their role as legitimate pollinators was largely dismissed until the last decade of the 20th century. STEINER (1998) showed that hopliine scarabs were the sole pollinators of *Moraea villosa* and its allies with similar flowers. GOLDBLATT *et al.* (1998b) examined the role of beetles as pollinators in a range of southern African herbaceous plants, including six *Moraea* species, emphasizing the role of convergent evolution as reflected in the same syndrome being expressed in many genera of both petaloid monocots and selected eudicot families (e.g., Asteraceae, Campanulaceae, Droseraceae). *Moraea*

species pollinated by hairy scarabs are in fact prominent components of a specialized pollination syndrome that BERNHARDT (2000) called the painted bowl syndrome. This system is dependent primarily on hairy beetles that visit salver- or bowl-shaped flowers lacking discernable scents and nectar but produce ample pollen advertised with highly contrasting pigmentation patterns, conveniently called beetle marks. This painted bowl syndrome is most diverse in the spring flora of the winter-rainfall zone of southern Africa and of the winter-early spring flora of the eastern Mediterranean Basin (DAFNI *et al.* 1990).

Thus, floral evolution and adaptive radiation in *Moraea* ultimately reflects the degree of modification to the architecture and presentation of the ancestral *Iris*-type meranthium. Where the meranthium architecture is pronounced and stereotyped, *Moraea* species are pollinated almost exclusively by medium-sized to relatively large bees with short or extended mouthparts. Where this architecture is almost completely suppressed and nectar is no longer secreted pollination is primarily the province of hairy scarabs. When characters of the *Iris*-type meranthium and the painted bowl syndrome intergrade the spectrum of potential pollinators is most likely to include a combination of beetles, short tongued dung and game flies and female, pollen-collecting bees of varying body sizes.

What is significant with regard to the floral evolution of *Moraea* is the absence of pollination systems taken for granted in other genera of the Iridaceae (and of some other families in Africa, notably *Disa* and *Satyrium* [Orchidaceae: e.g., JOHNSON *et al.* 1998] and *Pelargonium* [Geraniaceae: STRUCK 1997; MANNING & GOLDBLATT 1996]) of comparable taxonomic size or with only a fraction of the number of species found in *Moraea*. Systems not developed in *Moraea* are those exploiting sunbirds (*Nectarinia* spp.) and insects with exaggerated mouth-parts in which the proboscis is often several times the length of the animal's body. This includes pollination by the large-bodied, long-proboscid flies of the Nemestrinidae and Tabanidae, the long-tongued sphinx and noctuid moths, and large-bodied butterflies. Suppression of the

meranthium in *Moraea* has not led to the evolution of the elongated perianth tube, characteristic of such genera as *Babiana*, *Gladiolus*, *Hesperantha*, *Ixia*, *Lapeirousia*, *Nivenia*, and *Sparaxis*, that are dependent on the long-tongued pollinators listed above. Without an elongated nectar-filled tube *Moraea* has been unable to exploit modes of pollen dispersal effected by local guilds of birds and long-tongued insects.

Therefore, at first glance, pollination systems in *Moraea* appear less diverse than in the southern African genera of Geraniaceae, Iridaceae and Orchidaceae dependent on the elongation or severe reduction of the floral tube or spur. After all, bee and hairy scarab pollination systems also occur in species of *Babiana*, *Gladiolus*, *Hesperantha*, and several other genera. Nevertheless, we argue that pollination syndromes in *Moraea* show almost equal diversity because they have taken two co-adaptive pathways uncommon or absent in the genera with modified floral tubes. First, pollination by short-tongued dung and game flies, while present in *Moraea*, is completely absent in the seven genera listed in the preceding paragraph. The sapromyiophily (*sensu* FAEGRI & VAN DER PIJL 1979) expressed by some *Moraea* species has not evolved in other southern African genera of Iridaceae with extended floral tubes. It is also possible that pollination by the short-tongued potter wasps may also be unique to *Moraea* and its sister genus, *Ferraria* (BERNHARDT & GOLDBLATT in press).

Pollination by bees is also more complex in *Moraea* than in most of the other bee-pollinated genera of the African Iridaceae as it subdivides into two different modes of presentation exploiting different sets of bee taxa. *Moraea* species with well developed merantha are actually gullet flowers (FAEGRI & VAN DER PIJL 1979) dependent on medium- to large-bodied bee taxa with short or long tongues foraging primarily for nectar. Contact between the bee probing for nectar and the pollen-containing anther remains passive. In contrast, species in which the meranthium is suppressed have “lost” their “upper lip” due to the reduction of the stigmatic crests and the associated loss of the hidden position of the anthers. These species minimize nectar secretion but develop a prominent staminal column. Contact

between the bee and the anthers in these *Moraea* species is active as pollen is the primary reward encouraging female bees that actively harvest pollen via combing the anthers with their legs (BERNHARDT 1996). Few of the irid genera with floral tubes have evolved such nectar poor, “pollen flowers”. The only taxa to compare with the active pollen-collecting system in *Moraea* are *Romulea*, four species of *Gladiolus*, and two of *Babiana* that are nectar poor or lack nectar but present anthers to pollen-collecting *Apis mellifera*, Andrenidae, and Halictidae (GOLDBLATT *et al.* 1998b, 2002b; GOLDBLATT & MANNING unpubl. data).

If the adaptive radiation of floral forms and modes of floral presentation are so distinctive and actually represent trends towards specialized pollination systems why is the honeybee, *Apis mellifera*, an important pollinator of so many *Moraea* species regardless of floral type? With its hairy, relatively long body (13-14 mm) and long tongue it should be restricted to floral forms represented by the *Iris*-type (type I). Instead, honeybees are involved in the pollination of species representing floral types I-III (see above), regardless of the functional morphology, primary attractants, or rewards (nectar vs pollen) of the flower. Furthermore, the honeybee also appears to play some positive role as a pollen vector in some species with painted bowl type flowers (type IV, see above), a mode of presentation associated most commonly with beetles.

We remind the reader of two facts. First, honeybees are both native to Africa and are opportunistic floral foragers collecting both pollen and/or nectar from an unusually wide range of angiosperm species. That is, neuter workers are both polyphagic and polylectic. However, just as there is a division of labor of workers within a hive, based primarily on the physical age of each worker (SEELEY 1985), there is also a division of labor when workers forage on flowers (WINSTON 1987). That is, some workers forage primarily for nectar while others forage primarily for pollen on nectarless or nectar poor flowers (see HODGES 1974). Therefore, while all honeybees consume nectar and pollen, the foraging bout of a single worker may be a specialized one for either nectar or pollen.

Considering the size, tongue length and range of foraging behaviors of *Apis mellifera* workers it is not surprising that these insects visit most of the floral forms found in *Moraea*. Depending on the foraging mode, *Apis* workers, in general, are not deterred by a *Moraea* species offering copious pollen but no nectar or by a second species offering copious nectar while pollen is deposited passively and dorsally. Paradoxically, floral presentation does not deter successful foraging by *A. mellifera* even though two foragers in the same hive may not visit the same *Moraea* species at the same time. Considering the population density of a honeybee hive this is selectively advantageous for sympatric and coblooming *Moraea* species with different modes of floral presentation as they may now share the exact same species of pollen vector without ever competing for the same individuals.

The few self-compatible species of *Moraea* are evidently facultatively autogamous. So far, four of the eight self-compatible species known do receive visits from insects that can result in cross pollination. Three self-compatible species, *Moraea demissa* (= *Homeria tenuis* Schltr.), *M. flavescens*, and *M. pallida* deserve special mention. They are complex heterozygotes, the chromosomes of which form rings of various configurations at meiosis (GOLDBLATT 1980, 1981). The reproductive biology of these species has received little attention. Despite small flowers and facultative autogamy, at least *M. demissa* does receive visits from pollen-collecting bees which we assume also transfer pollen from other individuals and must contribute to its genetic diversity. Its diverse chromosome numbers, $2n = 10, 9$, and 8 , likewise show an unexpected genetic diversity for a facultatively autogamous plant.

POLLINATOR SHIFTS IN *MORAEA*

A generic phylogeny of *Moraea* using four plastid DNA regions (GOLDBLATT *et al.* 2000a) that includes 72 species, and second one (SAVOLAINEN *et al.* unpubl. data) using 175 species shows a pattern of repeated shifts in pollination systems. *Ferraria*, a southern African genus of some 12 species (BERNHARDT & GOLDBLATT in press) is the sister to the *Moraea* clade and the two genera are believed to have diverged in the Miocene, c. 25 mya. The ancestral pollination system in

Moraea, as discussed above, is the meranthium that exploits medium-sized to large bees with extended mouth-parts that forage for nectar and transfer pollen passively.

Within *Moraea*, the so-called *M. collina*-type flower has evolved repeatedly in several lineages across the genus, but is best developed and most diverse in the *Homeria* clade, in which three different pollination systems occur, the *M. collina*, *M. miniata*, and *M. ochroleuca* types (GOLDBLATT *et al.* 2000a). A second clade with the *Moraea collina*-type flower is nested in a separate lineage, the *M. polyanthos* clade, that also includes *M. deserticola* Goldblatt and *M. speciosa*. Typical *Homeria*-type flowers also characterize the entire *Galaxia* clade, as well as in one isolated species, *M. umbellata* Thunb., nested in the *M. linderi* Goldblatt/*M. margaretae* Goldblatt clade.

The *Moraea miniata*-type flower with the anthers borne well above the tepal limbs on a prominent column is again most frequent in the *Homeria* clade of the genus that includes *M. bifida*, *M. brachygyne*, *M. cookii*, *M. demissa*, *M. pendula*, *M. reflexa*, and several more species. Whether they comprise a single lineage within that clade is uncertain at present because of low bootstrap values in the molecular analyses. A second lineage with the *M. miniata*-type flower is nested in the *M. polyanthos* clade that includes the species clustered around *M. crispa* (including *M. pseudospicata*). Typical *M. miniata*-type flowers also occur in the clade that includes subgenus *Visciramosae* (the species pair *M. elsiae* Goldblatt and *M. simplex* Goldblatt & J.C.Manning), the entire *Hexaglottis* clade (*M. virgata* and its immediate allies), in *M. nana* (L.Bolus) Goldblatt & J.C.Manning which has a flower like that of *Hexaglottis* but belongs in a clade with *M. linderi* and *M. margaretae*, species that have a classic *Iris*-type flower, as well as in some isolated species nested in other clades: the species pair *M. herrei* L.Bolus and *M. rigidifolia* Goldblatt; *M. vlokii* Goldblatt; and *M. worcesterensis* Goldblatt.

The painted bowl flower and hopliine beetle pollination is developed in at least two lineages in subgenus *Vieusseuxia*, the *Moraea villosa* group (including *M. gigandra*, *M. loubseri*, and *M. tulbaghensis*) and in *M. insolens* and *M. cantharophila*, a species that may not be immediately

allied to *M. insolens*. All these species have long-lasting flowers that, except in *M. cantharophila* have pronounced beetle marks. Painted bowl-type flowers also occur in the *Homeria* clade in the related species pair, *M. comptonii* and *M. elegans*, in which they are highly scented and secrete nectar. The two species have a hopliine beetle/pollen-collecting bee pollination system. Two more species appear to have painted bowl-type flowers, *M. barnardiella* and *M. melanops*, a species pair of the *Galaxia*-group.

Pollination by dung, flesh and game flies, typical sapromyiophily (FAEGRI & VAN DER PIJL 1979) is restricted to two species, *Moraea lurida* (subgenus *Vieusseuxia*) and *M. ochroleuca* (the *Homeria*-clade). Curiously, both species have the diffuse nectary condition described above.

This brief survey of the taxonomic distribution of pollination systems in *Moraea* shows the repeated evolution of derived systems, as has been noted for other genera of the Iridaceae. Based on observations and capture of pollinators on all the main flower types in the genus, and inferring the pollination systems of species with similar floral presentation, we tentatively postulate that at least 18 shifts have occurred, one shift for every nine species. An estimate in the genus *Gladiolus* in southern Africa provides an even higher rate change of pollination system, one shift for every five species (GOLDBLATT *et al.* 2001). In *Babiana*, GOLDBLATT & MANNING (unpubl. data) postulate one shift for every six species. The tubular flowers of *Babiana* and *Gladiolus* have a wider range of pollination systems that include passerine birds, long-proboscid flies, large butterflies (only *Gladiolus*), sphinx moths, and hopliine beetles (only *Babiana*), as well as the ancestral nectar foraging bee system and the derived pollen collecting female bee system that is much more developed in *Moraea*.

By our estimate, 108 species of *Moraea* (55%) have an *Iris*-type flower. Flowers of the *M. collina*-type characterize 30 species (15%), while flowers of the *M. miniata*-type occur in 41 species (21%) of the genus. Just 14 species (7%) have painted bowl flowers and only two (1%) have *M. ochroleuca*-type flowers.

Geographic distribution of the flower types, and by extension, the pollination types, is some-

what surprising. Species with the *Iris*-type flower occur across the entire range of the genus. Other systems are largely confined to the southern African winter-rainfall zone that extends from southwestern Namibia in the north to Port Elizabeth, South Africa, in the southeast. Outside this comparatively small area, less than 6% of the entire range of the genus, only three species have a different flower, the *M. miniata*-type flower (in *M. cookii*, *M. pallida*, and *M. thomsonii*). The painted bowl and *M. ochroleuca*-type flowers have an even narrow range: they are restricted to the southwest of Western Cape Province of South Africa. These patterns may reflect the effects of competition for pollinators in an area where flowering in a rich and diverse flora is compressed into a short spring season, mostly August and September.

Acknowledgements

Support for this study by grants 5994-97, 6704-00, 7103-01, and 7316-02 from the National Geographic Society is gratefully acknowledged. We thank Robert BROOKS, University of Kansas, Holger DOMBROW, Worms, Germany, and Kim E. STEINER, California Academy of Sciences, for their many insect identifications; and Ingrid NÄNNI and Lendon PORTER for their help and companionship in the field.

REFERENCES

- BERNHARDT P. 1996. — Anther adaptation in animal pollination: 192-220, in D'ARCY W.D. & KEATING R.C. (eds), *The Anther: Form, Function, and Phylogeny*. Cambridge University Press, Cambridge, UK.
- BERNHARDT P. 2000. — Convergent evolution and adaptive radiation of beetle-pollinated angiosperms. *Pl. Syst. Evol.* 222: 293-320.
- BERNHARDT P. & GOLDBLATT P. in press. — The role of phylogenetic constraints in the evolution of pollination mechanisms in the Iridaceae of sub-Saharan Africa, in COLUMBUS J.T., FRIAR E.A., PORTER J.M., PRINCE L.M. & SIMPSON M.G. (eds), *Monocots: Comparative Biology and Evolution*. Vol. 1. Rancho Santa Ana Botanic Garden, Claremont, California, USA.
- BUCHMANN S.L. 1983. — Buzz pollination in angiosperms: 73-113, in JONES C.E. & LITTLE R.J. (eds), *Handbook of Experimental Pollination*. Van Nostrand Reinhold, New York.

- DAFNI A., BERNHARDT P., SCHMIDA A., IVRI Y., GREENBERG S., O'TOOLE C. & LOSITO L. 1990. — Red bowl-shaped flowers: convergence for beetle pollination in the Mediterranean region. *Israel J. Bot.* 39: 81-92.
- FAEGRI K. & VAN DER PIJL L. 1979. — *The Principles of Pollination Ecology*. Edition 3. Pergamon Press, New York.
- GOLDBLATT P. 1979. — Biology and systematics of *Galaxia* (Iridaceae). *J. S. African Bot.* 45: 385-423.
- GOLDBLATT P. 1980. — Uneven diploid numbers and complex heterozygosity in *Homeria* (Iridaceae). *Syst. Bot.* 5: 337-340.
- GOLDBLATT P. 1981. — Systematics and biology of *Homeria* (Iridaceae). *Ann. Missouri Bot. Gard.* 68: 413-503.
- GOLDBLATT P. 1986. — The *Moraea*s of Southern Africa. *Ann. Kirstenbosch Bot. Gard.* 14: 1-224.
- GOLDBLATT P. 1987. — Systematics of the southern African genus *Hexaglottis* (Iridaceae-Iridoideae). *Ann. Missouri Bot. Gard.* 74: 542-569.
- GOLDBLATT P. 1990. — Phylogeny and classification of Iridaceae. *Ann. Missouri Bot. Gard.* 77: 607-27.
- GOLDBLATT P. 1991. — An overview of the systematics, phylogeny and biology of the southern African Iridaceae. *Contr. Bolus Herb.* 13: 1-74.
- GOLDBLATT P. 1993. — *The Woody Iridaceae: Systematics, Biology and Evolution of Nivenia, Klattia and Witsenia*. Timber Press, Portland, Oregon.
- GOLDBLATT P. 1998. — Reduction of *Barnardiella*, *Galaxia*, *Gynandriris*, *Hexaglottis* and *Homeria* in *Moraea* (Iridaceae: Irideae). *Novon* 8: 371-377.
- GOLDBLATT P. 2001. — Phylogeny of the Iridaceae and the relationships of *Iris*. *Ann. Bot. (Roma)* 46: 1-16.
- GOLDBLATT P. & BERNHARDT P. 1999. — Pollination mechanics of *Moraea* species (Iridaceae) with a staminal column. *Ann. Missouri Bot. Gard.* 86: 47-56.
- GOLDBLATT P. & MANNING J.C. 1995. — New species of southern African *Moraea* (Iridaceae: Iridoideae), and the reduction of *Rheome*. *Novon* 5: 262-269.
- GOLDBLATT P. & MANNING J.C. 1996. — Aristeas and beetle pollination. *Veld & Flora* 82: 17-19.
- GOLDBLATT P. & MANNING J.C. 2000. — New species of *Moraea* (Iridaceae-Iridoideae) from southern Africa. *Novon* 10: 14-22.
- GOLDBLATT P. & MANNING J.C. 2002a. — Notes and new species of *Moraea* (Iridaceae: Iridoideae) from winter-rainfall southern Africa. *Novon* 12: 352-359.
- GOLDBLATT P. & MANNING J.C. 2002b. — Evidence for moth and butterfly pollination in *Gladiolus* (Iridaceae: Crocoideae). *Ann. Missouri Bot. Gard.* 89: 110-124.
- GOLDBLATT P., BERNHARDT P. & MANNING J.C. 1989. — Notes on the pollination mechanisms of *Moraea inclinata* and *M. brevistyla* (Iridaceae). *Pl. Syst. Evol.* 163: 201-209.
- GOLDBLATT P., MANNING J.C. & BERNHARDT P. 1995. — Pollination biology of *Lapeirousia* subgenus *Lapeirousia* (Iridaceae) in southern Africa: floral divergence and adaptation for long-tongued fly-pollination. *Ann. Missouri Bot. Gard.* 82: 517-534.
- GOLDBLATT P., MANNING J.C. & BERNHARDT P. 1998a. — Floral biology of bee-pollinated *Gladiolus* species in southern Africa. *Ann. Missouri Bot. Gard.* 85: 492-517.
- GOLDBLATT P., BERNHARDT P. & MANNING J.C. 1998b. — Pollination by monkey beetles (Scarabaeidae-Hopliini) in petaloid geophytes in southern Africa. *Ann. Missouri Bot. Gard.* 85: 215-230.
- GOLDBLATT P., MANNING J.C. & BERNHARDT P. 1999. — Evidence of bird pollination in Iridaceae of southern Africa. *Adansonia* sér. 3, 21 (1): 25-40.
- GOLDBLATT P., MANNING J.C. & BERNHARDT P. 2000a. — Adaptive radiation of pollination mechanisms in the African genus *Ixia* (Iridaceae: Crocoideae). *Ann. Missouri Bot. Gard.* 87: 564-577.
- GOLDBLATT P., MANNING J.C. & BERNHARDT P. 2000b. — Adaptive radiation of pollination mechanisms in *Sparaxis* (Iridaceae: Ixioideae). *Adansonia* sér. 3, 22 (1): 57-70.
- GOLDBLATT P., MANNING J.C. & BERNHARDT P. 2001. — Radiation of pollination systems in *Gladiolus* (Iridaceae: Crocoideae) in southern Africa. *Ann. Missouri Bot. Gard.* 88: 713-734.
- GOLDBLATT P., SAVOLAINEN V., PORTEOUS O., SOSTARIC I., POWELL M., REEVES G., MANNING J.C., BARRACLOUGH T.G. & CHASE M.W. 2002a. — Radiation in the Cape flora and the phylogeny of peacock irises *Moraea* (Iridaceae) based on four plastid DNA regions. *Molec. Phylog. Evol.* 25: 341-360.
- GOLDBLATT P., BERNHARDT P. & MANNING J.C. 2002b. — Floral biology of *Romulea* (Iridaceae: Crocoideae): a progression from a generalist to a specialist pollination system. *Adansonia* sér. 3, 24 (2): 243-262.
- GOLDBLATT P., NÄNNI I., BERNHARDT P. & MANNING J.C. 2004. — Floral biology of *Hesperantha* (Iridaceae: Crocoideae): shifts in flower color and timing of floral opening and closing radically change the pollination system. *Ann. Missouri Bot. Gard.* 91: 186-206.
- HODGES D. 1974. — *The Pollen Loads of the Honey-bee*. Bee Research Association, London.
- JOHNSON S.D., LINDER H.P. & STEINER K.E. 1998. — Phylogeny and radiation of pollination systems in *Disa* (Orchidaceae). *Amer. J. Bot.* 5: 402-411.
- KNUTH P. 1909. — *Handbook of Flower Pollination*. 3 (translated by AINSWORTH DAVIS J.R.). Clarendon Press, Oxford.
- MANNING J.C. & GOLDBLATT P. 1996. — The *Prosoeca peringueyi* (Diptera: Nemestrinidae) pollination syndrome in southern Africa: long-tongued flies and their tubular flowers. *Ann. Missouri Bot. Gard.* 83: 67-86.

- MARLOTH R. 1917. — *Flora of South Africa* vol. 1. Darter Brothers, Cape Town.
- MÜLLER H. 1883. — *The Fertilisation of Flowers*. MacMillan, London.
- OGDEN E.C., RAYNOR G.S., HAYERS J.V. & LEWIS D.M. 1974. — *Manual of Sampling Airborne Pollen*. Hafner Press, London.
- PÉREZ CHISCANO J.L. 2001. — Aspectos sobre fenología, reproducción y ecología de *Gynandriris sisyrinchium* (L.) Parl. (Iridaceae). *Stud. Bot. (Salamanca)* 20: 77-92.
- PERINGUEY L. 1902. — Descriptive catalogue of the Coleoptera of South Africa (Lucanidae and Scarabaeidae). *Trans. S. African Phil. Soc.* 12: 1-920.
- PROCTOR M., YEO P. & LACK A. 1996. — *The Natural History of Pollination*. Timber Press, Portland, Oregon.
- REEVES G., CHASE M.W., RUDALL P.J., FAY M.F., COX A.V., LEJEUNE B. & SOUZA-CHIES T. 2001. — Molecular systematics of Iridaceae: evidence from four plastid DNA regions. *Amer. J. Bot.* 88: 2074-2087.
- SEELEY T.D. 1985. — *Honeybee Ecology; a Study of Adaption in Social Life*. Princeton University Press, Princeton, New Jersey.
- SCOTT-ELLIOT G. 1891. — Notes on the fertilisation of South African and Madagascan flowering plants. *Ann. Bot.* 5: 333-405.
- STEINER K.S. 1998. — Beetle pollination of peacock moraeas in South Africa. *Pl. Syst. Evol.* 209: 47-65.
- STRUCK M. 1997. — Floral divergence and convergence in the genus *Pelargonium* (Geraniaceae) in southern Africa: ecological and evolutionary considerations. *Pl. Syst. Evol.* 208: 71-97.
- VOGEL S. 1954. — Blütenbiologische Typen als Elemente der Sippengliederung. *Bot. Stud.* 1: 1-338.
- WINSTON M.L. 1987. — *The Biology of the Honey Bee*. Harvard University Press, Cambridge, Massachusetts.

*Submitted on 11 June 2004;
accepted on 5 April 2005.*