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REVIEW ARTICLE

African pollination studies: where are the gaps?

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Abstract. The literature on African pollination biology is reviewed. It is found that relatively little work has been done on pollination biology in Africa, and a very small proportion of pollination relationships has so far been studied. Much of the research which has been done is of an evolutionary nature. Very little work has been conducted at the community level and comparatively little applied work, either to agriculture or conservation, was encountered. Most research has been conducted in South Africa, in particular, from the Cape region, which is the only part of Africa for which a reasonably comprehensive body of work on pollination biology exists. In a number of instances results of African studies challenge conventional understanding of pollination biology. It is argued that as more work on pollination is done in Africa, more differences between African systems and the rest of the world, particularly the North temperate regions will be found and changes to the overall conceptualization of pollination systems in different ecosystems are likely to ensue. A more thorough understanding of pollination biology would also make an important contribution to food security and conservation of biodiversity on the continent. Scientists working in fields other than pollination biology, and amateurs, should be encouraged to contribute to the groundwork of African pollination biology by the documentation of pollination relationships.

Key words: pollinators, pollination syndrome, breeding system, biodiversity, pollinator conservation, crop pollination, African studies

Résumé. Une revue bibliographique de la biologie de la pollinisation en Afrique est présentée. On constate que relativement peu de travaux ont été réalisées sur la biologie de la pollinisation en Afrique et qu'une très faible proportion des relations de pollinisation a été étudiées. La plupart des recherches effectuées ont porté sur des approaches évolutives. Très peu de travaux ont été conduits à l'échelle de la communauté et on a trouvé peu de travaux appliqués aussi bien dans le domaine de l'agriculture que de la conservation. La plupart des recherches ont été menées en Afrique du Sud, en particulier, dans la region du Cap, qui est la seule région d'Afrique pour laquelle on dispose d'une quantité de données acceptables sur la biologie de la pollinisation. Dans un certain nombre de cas, les résultats des études Africaines remettent en question les connaissances conventionnelles sur la biologie de la pollinisation. Ils indiquent que plus on conduira de travaux sur la

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pollinisation en Afrique plus de differences seront mises en évidence entre les systèmes Africains et le reste du monde, en particulier avec les régions tempérées septentrionales et que cela conduira à une modification des théories sur les systèmes de pollinisation dans les différents écosystèmes. Une meilleure connaissance de la biologie de la pollinisation pourrait également contribuer à améliorer la production agricole et la préservation de la biodiversité sur le continent. On devrait encourager le développement des recherches sur la biologie de la pollinisation en particulier dans le domaine des relations de pollinisation chez les scientifiques travaillant dans des domaines de recherches autres que la biologie de la pollinisation ainsi que chez les amateurs.

Mots clés: Pollinisateurs, syndrome de pollinisation, système de reproduction, biodiversité, préservation des pollinisateurs, pollinisation des cultures, études africaines

Introduction

Growing awareness of the vital role of pollination in agricultural production and plant conservation and increasing alarm over threats that human activities pose to animal pollinators have brought pollination to the top of the research agenda (Buchmann and Nabhan, 1996; Cane and Tepedino, 2001; Williams, 2002). Animal pollination is a vital step in the reproduction of most flowering plants. Most crop plants, except cereals, are either completely dependent on pollinators to produce fruit or show improved yield as a result of their activities (Roubik, 1995). There are many recorded instances of pollination deficit reducing agricultural productivity (Kevan and Phillips, 2001). Conservation of pollinators is necessary for the successful conservation of plants and decline of pollinators is considered as a potential threat to plant conservation (Thompson, 2001). Pesticide use, introduction of exotic pollinators, pests, diseases, habitat fragmentation and degradation will all threaten pollinators and the services they provide (Roubik, 1995; Delaplane and Mayer, 2000; Donaldson, 2002). Decline of pollinator populations and related declines in pollination rates are therefore regarded as potential threats to both agriculture and conservation (Thompson, 2001; Williams, 2002).

Although wind pollinated plants are not affected by animal pollinators, understanding of wind pollination may be used to improve pollination in crops such as cereals and conifers (El-Kassaby and Reynolds, 1990; Owens *et al.*, 1998). As with animal pollinated plants, wind-pollinated plants may also be prone to the effects of habitat fragmentation (Knapp *et al.*, 2001).

Pollination biology is also of general ecological and conservation relevance as changes in plant population growth rates, population size and community composition involve reproduction. Population size and density markedly affect pollination success (Groom, 2001; Lennartsson, 2002; Wilcock and Neiland, 2002).

Developing nations are particularly vulnerable to food crises and often struggle to allocate resources to conservation. In Europe and North America comprehensive information on pollination relationships and breeding systems has existed for around 100 years (Knuth, 1898–1905 in German and the English translation in 1906–1909, Proctor *et al.*, 1996a,b) but in Africa's developing nations and much of Asia and Latin America, pollination biology, like most other scientific fields, is less well researched. Although there are parts of the developing world where substantial progress has been made, even in the best-researched regions a sound understanding of pollination biology has not yet been achieved. The body of research that has been generated from Brazil, both in bee biology and pollination ecology is substantial (Kevan and Imperatriz-Fonseca, 2002) and is an exception from which other developing nations can draw inspiration. But even in this case there are gaps in taxonomic and geographic coverage; synthesis between regions is problematic and information is generally inadequate to make recommendations for management for either conservation or crop pollination (Pinheiro-Machado *et al.*, 2002). In Africa extensive work remains to be done to bring our understanding of pollination in line with that in the developed world. Yet an improved understanding of pollination can make a substantial contribution to two key sectors of African economies, agriculture and conservation, thus yielding multiple benefits. This review examines the literature on pollination biology from this continent and attempts to identify the areas in which research is most needed.

Methods

A literature search was conducted, using the Science Citation Index from the years 1990–2000 (Institute for Scientific Information, 2000) and all years up to 2000 in the NISC African Studies index (NISC, 2001) as a starting point. The reference lists of the literature found were also searched to obtain further sources. This was done by James Rodger (JGR) and he examined these papers for the purpose of this review. A second set of papers were examined by Barbara Gemmill (BG), drawn primarily from the bibliographies of three seminal texts on pollination (Crane and Walker, 1984; Free, 1996; Proctor *et al.*, 1996a). A comprehensive cover of the literature published in the referred scientific journals has been attempted but some articles have doubtlessly been omitted. On the other hand certain conference proceedings, research reports and lay journals have also been included. Articles dealing with flower visiting have not been included unless conclusions about pollination were actually drawn. Likewise, articles dealing with flower and pollen morphology and nectar composition have been excluded except where these are linked to pollination either by direct observation or by inference from observations of pollen being carried by the pollinating agent under natural conditions. For the purpose of this review, Madagascar is included in Africa, except where specifically mentioned as not included. While this review has not taken into account the entire knowledge of pollination in Africa, it is felt that the sample accounts for the majority of information and that the conclusions drawn are valid.

Each article was categorized according to subject matter, the type of article, geographic area and plant and pollinator groups dealt with. Under each of these headings an individual record might fall into more than one category and in some cases overlapping categories have been used.

The following categories have been recognized under subject matter: pollinator type, pollination syndrome and plant speciation, plant breeding system, agricultural/horticultural application, conservation application and pollinator and plant community ecology. The types of papers recognized were: research generating observational data (observational research), research in which manipulative work was conducted (manipulative research) and reviews.

In order to assess the extent to which pollination biology has been investigated in plant families and higher taxonomic groups (monocotyledons, dicotyledons and spermatophytes) on the mainland of Africa (excluding Madagascar) an index of intensity of study, which is an estimate of the percentage of species studied, was calculated according to the following formula, using the species examined by JGR (The family studied but not the species was noted for the papers examined by BG).

Index of percentage intensity of study = (number of species studied × 100)/(number of species in central African region (Stork and Le Brun, 1997) + number of species in southern African region (Leistner, 2000), with the number of species in central African region + number of species in southern African region being an estimate of the number of species in Africa. This can only be regarded as a rough approximation as it does not include North Africa and some species occurring in central Africa will also occur in southern Africa.

A species was counted as studied if an original report on its pollination biology was included in the review. Examples cited in review articles were excluded. As Vogel (1954) was not available in English, the accounts published in that work have not been used.

The geographic categorization that has been used is: North Africa, East Africa, West Africa, Central Africa, Southern Africa and Madagascar. Madagascar's long separation from continental Africa has given rise to floristic peculiarities (Guillaumet, 1984), thus justifying its recognition as a region.

At the continental level, South Africa's Cape region is floristically unique by virtue of its remarkable species diversity and its species composition in terms of plant families and growth forms (Goldblatt and Manning, 2000). South Africa can therefore be clearly divided into two regions: the Cape region and the rest of the country (non-Cape region) as defined by Goldblatt and Manning (2000). For the papers examined by JGR, the southern African region was thus further broken down in to the following categories: papers covering southern Africa, South Africa (the whole country), Cape region in South Africa and non-Cape region in South Africa.

Results and Discussion

Subject matter

Pollinator type, pollination syndrome and speciation and breeding systems

In the 355 papers reviewed, pollinator type, pollination syndrome and speciation were the most common subfields investigated, followed by breeding systems (Fig. 1). Much of this sort of information was already known for Europe and North America a century ago, summarized by Knuth in his classic work *Handuch der Blütenbiologie*

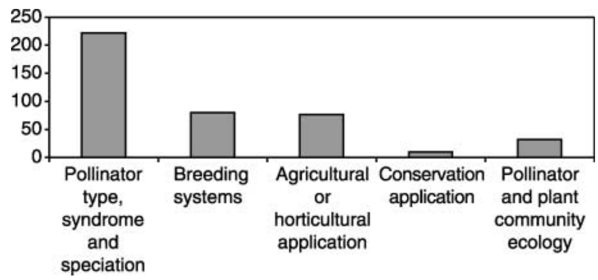

Fig. 1. The numbers of papers on pollination biology in Africa, published in different sub-fields of pollination biology

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(1898–1905) and translated into English as *Handbook of Flower Pollination* (1906–1909) (Proctor *et al.*, 1996a,b). It is an indication of the general lack of information on pollination relationships in Africa that such a large component of research is still directed towards investigation of the nature of relationships and breeding systems. The high proportion of papers in these subfields also indicates a systematic and evolutionary bias in studies of pollination in Africa. A review of agricultural pollination in South Africa by Donaldson (2002) is in agreement with this finding.

Community ecology

Only 32 papers dealing with community ecology were encountered (Fig. 1). Understanding of plant and pollinator community composition with respect to pollination syndrome and pollinator type has been greatly enhanced elsewhere (Proctor *et al.*, 1996b), but in Africa few such studies have been conducted (see Stone *et al.* (1998) for acacia in East Africa and Rebelo (1987a) for fynbos in South Africa). Some features of African pollination which apply at the community as well as the regional level are noted below in the section 'Africa is different'. Effects of invasive alien plants and pollinators are also community level issues (see section 'Applied studies').

Applied studies: Agriculture

Less than 20% of the papers had an applied component, whether of agricultural, horticultural or conservation relevance. Yet this type of research is vitally important for food security. In crops, pollination by animals may be essential for fruit production (e.g. date palm and watermelon) or to improve yields (e.g. tomato and broad beans). In stem and root crops like radish and chicory pollinators may still be needed to produce seed. Pollinators are vital for hybrid seed in many crops (e.g. sunflower and onions) (McGregor, 1976; Roubik, 1995). A provisional list of commercially important commodities within Africa which are known to have a high dependence on animal pollination is given in Table 1.

While commercial pollinating companies operate in certain countries such as South Africa and Zimbabwe, their expertise is not usually published in scientific journals. A more thorough search of lay agricultural journals could increase the number of studies obtained in this category. The bibliography accompanying this article will be available on the API website (www.elci.org/api), and will be searchable by species, crop commodity, and region such that literature specifically addressing pollination of crops in Africa can be identified; additions are welcomed.

To a certain extent, information on agricultural crop pollination in Africa can be obtained from general reference works on pollination around the world (Table 1). For example, Free (1996) is a crop-by-crop account of pollination systems and pollination needs and remains an especially comprehensive and relevant reference work for agricultural pollination globally. Others are Crane and Walker (1984) and McGregor (1976, but continually updated at http://66.181.86.172/beeculture/book/). However, this literature reflects the overwhelming focus and dependence on honeybees up to the present in agricultural pollination research. Out of over 2600 references included in the Free reference, over 87% are on honeybee pollination of crops. There are only 58 references (2.2% of all) on bumblebees, 6 (0.2%) on stingless bees, 90 (3.4%) on solitary bees and 16 (0.6%) on flies, 149 (5.6%) on insect pollinators in general and 24 (0.8%) on other pollinators which included butterflies, beetles, wasps, thrips, midges, weevils, ants and bats (Partap, 2003).

A review of agricultural pollination in South Africa (Donaldson, 2002) also finds most South African pollination work has dealt with descriptions and evolutionary studies of pollination in indigenous plants and agricultural studies have focused almost exclusively on honeybees. Little research has been conducted on the interactions of other native pollinators and crops. Donaldson (2002) states that pollinator decline has not been assessed but research into varroa mite and problems stemming from introduction of Cape honeybees (*Apis mellifera capensis*) into the rest of the country (previously exclusively occupied by *A. mellifera scutellata*) is ongoing. He also reports that two introduced insects, the Argentine ant *Linepithima humile* and the yellow-jacket wasp *Vespula germanica* are regarded as potential threats to indigenous pollinators but their impacts have not been investigated.

The detrimental effects of pesticide applications to crops during flowering are well documented. (Delaplane and Mayer, 2000) but other uses of pesticide, such as spraying of malaria mosquitos (Pankiw and Jay, 1992), may also be detrimental to pollinator populations. We did not come across any literature on the effects of pesticides on pollinators in Africa and this subject also receives little attention from Donaldson (2002). This suggests that the impact of pesticides on pollinators is almost completely unknown in Africa.

The emphasis in the literature on honeybees is a reflection of their abundance and manageability in farming systems worldwide. Although commercial pollination in Africa only occurs on a wide scale in a

Table 1. Important commercial commodities within Africa known to benefit from animal vectors for pollination

Commodity	Free, 1996 pages	Crane and Walker, 1984 pages	McGregor, 1976 http://66.181.86.172/beeculture/book url	Known pollinator(s)
GRAIN LEGUMES				
Bambara groundnut, *Voandzeia subterranea*	342–3	73	–	Self pollinated and self fertile but presence of ants increased productivity in Ghana
Broad bean, *Vicia faba* var. *major*	298	23	/chap4/broad.html	Self and bees
Common (field) bean, *Vicia faba* var. *minor*	298	23	/chap4/broad.html	Self and bees
Cowpea, *Vigna unguiculata*	341–2	107	/chap4/cow.html	Self and bees
Lima bean, *Phaseolus lunatus*	269–70	22	/chap4/lima.html	Self and bees
Pigeon pea, *Cajanus cajan*	317–20	107	/chap4/pig.html	Probably self and bees but not well known
VEGETABLES				
Amaranth, *Amaranthus* spp.	–	–	–	Not known
Aubergine/eggplant, *Solanum melongena*	503–4	62	/chap6/eggplant.html	Bees other than honeybees
Chayote, *Sechium edule*	–	40	/chap6/chayote.html	Not known but insects are necessary
Cucumber, *Cucumis sativus*	196–201	58	/chap6/cucumber.html	Bees
Hot/sweet pepper, *Capsicum frutescens/annum*	499–500	110	/chap6/pepper.html	Self and bees but not well known
Karela, *Momordica charantia*	208	–	/chap6/balsam.html	Bees and beetles
Okra, *Abelmoschus esculentus*	352–4	100	/chap6/okra.html	Self, bees, wasps, flies, beetles, birds but no information from Africa
Oyster nut, *Telfairia pedata*	–	–	–	Not known
French bean, *Phaseolus vulgaris*	270	24	/chap4/beans.html	Self and bees
Field pea, *Pisum sativum*	338–9	107	–	Self and bees
Pumpkin, squash, marrow, *Cucurbita*	203–7	69	/chap6/pumpkin.html	Bees
Tomato, *Lycopersicon esculentum*	492–8	137	/chap6/tomato.html	Self and large bees
FRUIT CROPS				
Annon fruit (custard apple, cherimoya), *Annona squamosa*	129	40	/chap9/cherimoya.html	Beetles
Apple, *Malus domestica*	434–45	16	/chap5/apple.html	Bees
Avocado, *Persea americana*	240–4	19	/chap5/avocado.html	Bees, wasps, flies
Borassus palm, *Borassus flabellifer*	–	32	–	Not known
Breadfruit, *Artocarpus altilis*	372	33	–	Not well known; not known at all in Africa
Cape gooseberry, *Physalis peruviana*	504	–	–	Not known
Carambola, *Averrhoa carambola*	391	35	/chap9/carambola.html	Bees and other insects
Citrus, *Citrus*	479–85	44	/chap5/citrus.html	Bees and other insects
Cherry, *Prunus avium*	431–66	41	/chap5/cherry.html	Bees

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Table 1. *Continued*

Commodity	Free, 1996 pages	Crane and Walker, 1984 pages	McGregor, 1976 http://66.181.86.172/beeculture/book url	Known pollinator(s)
Date palm, *Phoenix dactylifera*	401–2	61	/chap5/date.html	Not known
Fig, *Ficus carica*	373–8	65	/chap5/fig.html	Fig wasps
Guava, *Psidium guajava*	386	73	/chap7/guava.html	Self, bees and other insects
Litchie, *Litchi chinensis*	487–8	88	/chap5/litchi.html	Bees, flies, ants and wasps
Mango, *Mangifera indica*	124–8	90	/chap5/mango.html	Not well understood
Marula, *Sclerocarya birrea*	–	–	–	Not known
Melon, *Cucumis melo*	190–6	92	/chap6/muskmelon.html	Bees
Watermelon, *Citrullus lanatus*	201–3	93	/chap6/watermelon.html	Bees
Natal plum, *Carissa grandiflora*	131–2	98	–	Not known
Papaya, *Carica papaya*	137–9	103	/chap5/papaya.html	Hawkmoths, skipper butterflies
Passion fruit, *Passiflora edulis*	408–9	104	/chap5/passionfruit.html	Large bees
Peach, *Prunus persica*	431–66	108	/chap5/peach.html	Self and bees
Pear, *Pyrus communis*	431–66	108	/chap5/pear.html	Bees
Plum, *Prunus* spp.	431–66	113	/chap5/plum.html	Bees
Strawberry, *Fragaria × ananassa*	425–30	130	/chap7/strawberry.html	Bees but no information from Africa
Tamarind, *Tamarindus indica*	340–1	134	–	Not known in Africa (*Apis dorsata* in Asia)
NUT CROPS				
Cashew nut, *Anacardium occidentale*	122–4	37	/chap5/cashew.html	Flies, ants and bees
Macadamia nut, *Macadamia integrifolia*	418–20	89	/chap5/mac.html	Bees, wasps, beetles
OIL CROPS				
Castor, *Ricinis communis*	226–7	38	–	Wind and bees
Coconut, *Cocos nucifera*	52	52	/chap5/coconut.html	Wind and bees
Groundnut, *Arachis hypogaea*	314–7	72	/chap3/peanut.html	Self but bees and thrips seen to increase production in Congo
Niger seed, *Guizotia abyssinica*	149, 161	98	/chap9/niger.html	Bees but not well known
Oil palm, *Elaeis guineensis*	398–401	99	/chap5/oil.html	Beetles
Safflower, *Carthamus tinctorius*	145–8	123	/chap9/safflower.html	Self and bees
Sesame, *Sesamum indicum*	410–11	127	/chap9/sesame.html	Self and bees
Shea, *Butryospermum pardoxum*	–	–	–	Not known
Soybean, *Glycine max*	325–9	27	/chap4/soy.html	Self and bees
Sunflower, *Helianthus annus*	–	132	/chap9/sun.html	Bees and other insects
BEVERAGE/STIMULANT CROPS				
Cacao, *Theobroma cacao*	504–14	51	/chap5/cacao.html	Ceratopogonid midges, thrips, ants
Cola nut, *Cola acuminata* and *nitida*	–	81	/chap7/kolanut.html	Flies but not well known
Coffee, *Coffea arabica*	475–8	53	/chap7/coffee.html	Self and bees
FIBRE/CONTAINER CROPS				
Cotton, *Gossypium* spp.	354–9	55	/chap9/cotton.html	Self, but bees increase production
Bottle gourd, *Lagenaria siceria*	207–8	68	/chap6/white.html	Hawkmoths, bees, bats
Kapok, *Ceiba petandra*	134–5	128	–	Bats, hawkmoths
Raffia palm, *Raphia* spp.	–	117	–	Not known

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Table 1. *Continued*

Commodity	Free, 1996 pages	Crane and Walker, 1984 pages	McGregor, 1976 http://66.181.86.172/beeculture/book url	Known pollinator(s)
FORAGE CROPS				
Acacia tortilis pods	–	–	–	Bees other than honeybees, butterflies, wasps
Desmodium	–			Not known
Egyptian clover, or berseem, *Trifolium alexandrinum*	271–97	30	/chap3/berseem.html	Bees
Indigofera	–	–	–	Bees other than honeybees, small butterflies
Stylosanthus	–	–		Not known
AGROFORESTRY CROPS				
Calliandra calthyrsus	–	35	–	Bees
Gliricidium sepium	–	–	–	Not known
Grevillea robusta	–	128	–	Not known
Leucaena leucophala	–	–	–	Not known
Sesbania sesban	–	–	–	Not known
COSMETICS				
Bixa, *Bixa orelllana*	–	–		Not known
Loofah sponge, *Luffa cylindrica*	208	85	/chap6/veg.html	Moths and butterflies, possibly bees
PESTICIDES				
Mexican marigold, *Tagetes lucida*	–	–	–	Not known
Neem, *Azadirachta indica*	–	–	–	Not known
Pyrethrum, *Chrysanthemum cinerariifolium*	148	116	/chap9/pyrethrum.html	Beetles and flies, also bees; more potent insecticide is derived when flowers are visited by insects
Rotenone, *Tephrosia vogelii*	–	136	/chap9/tephrosia.html	Not known
SPICES				
Black pepper, *Piper nigrum*	412–13	109	/chap9/black.html	Not well known
Vanilla, *Vanilla planifolia*	389–90	141	/chap9/vanilla.html	Specialized bees in area where vanilla is indigenous; largely by hand within Madagascar and Africa

few countries like South Africa and Zimbabwe, various initiatives to develop apiculture for pollination and honey are underway. It has, however, been widely argued that agriculture is overly dependent on honeybees for pollination, despite their unsuitability to many crops (Roubik, 1995; Kearns *et al.*, 1998; O'Toole, 2002; Westerkamp and Gottsberger, 2002). In several crops important within Africa (such as aubergines, tomatoes, peppers, papaya and passion fruit among others) we know that honeybees are not effective pollinators, and the focus must turn to alternative, wild species of pollinators. As will be discuss below, native pollination syndromes in Africa often differ from the conventional typologies of pollination systems and these differences may extend to agricultural pollination systems as well. Donaldson (2002) concludes by emphasizing the need for research to evaluate where non-honeybee pollinators are most likely to be important for crop pollination and the promotion of practices for integrating pollinator conservation into agriculture.

Applied studies: Conservation

Only nine of the papers examined dealt with conservation applications of pollination biology, yet for plant species to be effectively conserved, their pollination systems must also be conserved. The emerging concern that invasive plants may

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threaten reproduction of indigenous plants through competition for pollinators is only beginning to be addressed worldwide (Richardson, 2000; Ghazoul, 2002) and is of great potential importance to Africa, especially as most countries do not have the resources to effectively combat plant invasions. Similarly, introduced pollinators may have a detrimental effect on indigenous species through competition for floral resources.

Habitat fragmentation has complex effects on plant reproduction (e.g. Lamont *et al.*, 1993; Donaldson *et al.*, 2002; Lennartsson, 2002). It affects both plant and pollinator populations and may reduce a plant's reproductive success by reduction or extinction of pollinator populations (e.g. Donaldson *et al.*, 2002), reduced visitation of plants in fragments (e.g. Lamont, 1993; Aizen and Feinsinger, 1994) or by inbreeding depression (Lennartsson, 2002). See Field and Johnson (this volume) for a thorough review on the effects of fragmentation on pollination. These processes affect plant species to varying extents depending on the nature of fragmentation, the biology of the plants and the biology of the pollinators.

A notable study by Donaldson *et al.* (2002) of fragmentation of Renosterveld (a shrubby vegetation with an important grass component and high diversity of geophytes) by wheatfields in South Africa's Cape region found that species were affected differently by fragmentation. Plants with specialized pollination systems are predicted by theory to be more vulnerable to fragmentation effects than those with generalized pollination systems. This was supported in the case of the specialist orchid *Pterygodium catholicum*, pollinated only by the oil-collecting bee *Rediviva gigas*, which produced fruit only in the largest fragments. However, reproduction of *Gladiolus liliaceus* (Iridaceae), a plant pollinated by a single species of noctuid moth was unaffected by fragmentation, possibly because the pollinator, *Cucilla extricata*, has a broad larval host range which may buffer its populations against the effects of fragmentation. *Trachyandra hirsuta* (Asphodelaceae), which has a generalized pollination system involving bees, flies and beetles suffered significantly lower fruit production in fragments while three other species with generalized pollination systems were not affected. One of these, *Ornithogalum thyrsoides* (Hyacinthaceae), is self-compatible and autogamous. Selfed seeds of this species are highly germinable suggesting that autogamy and self-compatibility compensate for lack of pollinators. Another complication was that population size was not correlated with fragment size and in all instances *O. thyrsoides* and *Babiana ambigua* showed higher reproduction in larger populations irrespective of fragment size. In addition, differences in fragmentation impacts, vegetation cover and grass cover were found to be much more important than size in determining pollinator species richness and composition. Distance from habitat mainland, rockiness, vegetation cover and grass cover were found to be more important than fragment size in explaining occurrence of pollinator species. This study illustrates the complex nature of pollination in fragmented landscapes: the effects of fragmentation on pollination is a result of interaction between the effects on pollinators and plants, and cannot be predicted unless thorough knowledge of the biology of the pollinators and plants and the details of the fragmentation process (fragment size distribution, distances from habitat 'mainland', heterogeneity etc.) are integrated in each case. Since very often neither pollinators nor plants occur elsewhere (both the oil-collecting bee genus, *Rediviva* and the orchid *P. catholicum* in the example above are known only from southern Africa) it is essential that research of this nature should be conducted in Africa.

The evolutionary history of Africa has been one of wildly fluctuating climates and habitat extents, in which land-locked 'islands' of high biodiversity and endemism—such as the Miombo-Mopane woodlands of southern Africa, and the Eastern Arc Mountains of East Africa have served as natural centres of species conservation (Kingdon, 1989). The fact that these centres of diversity are also areas of high population pressures means that habitat fragmentation must be a major concern. The work of Donaldson *et al.* (2002), bears replication throughout the continent.

Types of paper

Out of a total of 355 research papers only 82 included manipulative (experimental) work (Fig. 2). Thus, there is a high proportion of observational (non-manipulative) studies in this field. Yet pollination biology is a field that lends itself to manipulation. This underlines the basic state of pollination biology in Africa. While simple observation may be a

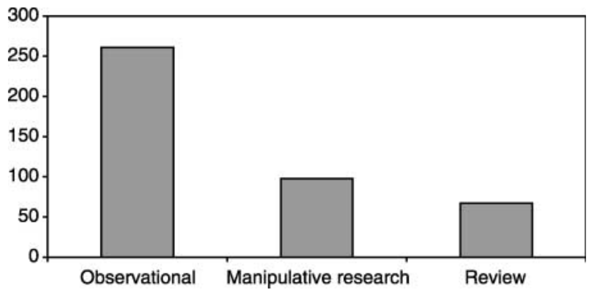

Fig. 2. The types of pollination biology studies in the literature of pollination biology in Africa

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necessary precursor to manipulative study, manipulative study is often necessary for hypothesis testing. There is scope for considerably more hypothesis testing and deductive science than has been conducted in the literature reviewed. The remaining papers were of a review nature (69 out of 355). These include nine papers published in the form of a synthesis report for pollination biology of the Cape flora (Rebelo, 1987a) and a number of taxonomic revisions in which pollination biology of the group concerned was reviewed.

Plant and pollinator groups

It is estimated that there are more than 45,000 species of vascular plants in Africa, and most of these are seed plants (Beentje *et al.*, 1994). For the purpose of the following analysis, we have used an estimate of the total number of described species in Africa of 48,274 (total number of species in central African region) (Stork and Le Brun, 1997) + number of species in southern African region (Leistner, 2000).

The papers examined by JGR contained information on the pollination biology of 673 species of these, giving an index of percentage intensity of study of 1.4% (Table 2). While this is no doubt an underestimate of the number of species about which information is available, even if the true figure was several times larger (which seems unlikely) African pollination biology still appears to be drastically understudied compared to Europe where information exists on a larger proportion of known species (Procter *et al.*, 1996). The situation in other regions of the developing world is likely to be similar to that in Africa and we suggest that similar, comparative percentages of intensity of study from other regions might usefully inform pollinator conservation initiatives and the gaps they must seek to address.

From the 219 articles reviewed by JGR it was possible to calculate indices of 'percentage of intensity of study' for 50 families (as circumscribed in Leistner, 2000) (Table 2). Of the 20 largest of these families (according to index of size) only Iridaceae, Proteaceae and Geraniaceae have indices of intensity of study higher than 10% and, apart from these, only Orchidaceae and Rubiaceae have indices of intensity of study exceeding 3%. Many of the largest families on the continent such as Fabaceae (% index of study = 0.82) and Asteraceae (% index of study = 0.34) remain very poorly studied. Some relatively large families such as the wind pollinated Cyperaceae appear not to have been studied at all; in other areas such as the Arctic and the Florida Everglades, an understanding of Cyperaceae breeding systems is critical to managing wetland resources. A number of small families like Podocarpaceae and Strelitziaceae have scored high indices of intensity of study because the few studies conducted in them have addressed a high proportion of their species due to their small size. In addition, more monocotyledonous species have been studied than dicotyledons, despite dicotyledons account for a greater part of the flora.

Where floral characters are important in phylogeny and evolution, as in Orchidaceae (Johnson, 1997a,b) and Iridaceae (Goldblatt and Manning, 1999; Goldblatt *et al.*, 2000), pollination biology tends to be well studied. For systematists working in these groups research into pollination biology is integral to systematic research. The discovery of unusual pollination syndromes such as the oil-collecting bee and long proboscid fly systems (Table 3) also seems to have stimulated work in the families in which they occur (Orchidaceae, Scrophulariaceae, Geraniaceae) (Table 2).

The wind pollinated families Cyperaceae, Restionaceae and Poaceae are highly speciose. Grasses are a dominant group both in savannas and grasslands, sedges dominate in wetlands and Restionaceae are one of the three most dominant families in the Cape region, yet hardly any work has been conducted on these families in Africa (Table 2). Use of grass pollen by bees is reported in Kenya (Bogdan, 1962) and South Africa (Immelmann and Eardley, 2000) and may prove to be more important in Africa than in other continents when investigated further. By virtue of their ecological dominance it is likely that their pollination biology will be of great consequence for ecology in Africa. Veld management, for instance, is often concerned with promotion of grass species beneficial for grazing and the pollination biology of grasses, including aspects such as self-compatibility and effective pollination distance, has important implications for managing transitions between dominance of different species.

Geographic areas in which studies were conducted

The vast majority of the studies considered were conducted in southern Africa and in particular, in the Republic of South Africa (Figs 3 and 4). A considerable quantity of African research languishes in university libraries in the form of unpublished postgraduate theses, and we may not have been able to access much of the more localized research. It nevertheless seems certain that a disproportionate amount of research is conducted in South Africa.

West Africa does not fare quite as poorly as East and North Africa, because much of the economic pollination work (on cocoa and oil palm) has been carried out there; but in comparison to southern Africa and most other regions of the world, the

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Table 2. Intensity of study of spermatophytes, dicotyledons, monocotyledons and those plant families which have been studied in Africa (Index of size = number of species in central African region (Stork and Le Brun, 1997) + number of species in southern African region (Leistner, 2000); Index of percentage intensity of study = (number of species studied × 100)/(Index of size)

Plant group	Sum of numbers of species in Central and southern Africa	Number of species in papers (original accounts)	Index of percentage intensity of study
Spermatophyta	48300	673	1.39
Dicotyledons	31920	268	0.84
Monocotyledons	16354	405	2.48
Fabaceae	4520	37	0.82
Asteraceae	4160	14	0.34
Euphorbiaceae	1803	5	0.28
Orchidaceae	1774	73	4.12
Mesembryanthemaceae	1688	3	0.18
Poaceae	1550	1	0.07
Apocynaceae	1521	10	0.66
Acanthaceae	1512	2	0.13
Scrophulariaceae	1236	26	2.10
Iridaceae	1186	287	24.20
Lamiaceae	873	9	1.03
Asphodelaceae	599	4	0.67
Hyacinthaceae	526	5	0.95
Rubiaceae	410	17	4.15
Proteaceae	398	65	16.33
Polygalaceae	355	1	0.28
Geraniaceae	338	34	10.06
Amaryllidaceae	334	6	1.80
Crassulaceae	332	2	0.60
Restionaceae	323	3	0.93
Campanulaceae	316	2	0.63
Commelinaceae	311	5	1.61
Thymelaeaceae	278	1	0.36
Boraginaceae	266	3	1.13
Rhamnaceae	243	1	0.41
Rosaceae	228	1	0.44
Loranthaceae	223	1	0.45
Moraceae	200	10	5.00
Sapotaceae	159	1	0.63
Araceae	140	5	3.57
Hypoxidaceae	117	2	1.71
Balsaminaceae	113	8	7.08
Colchicaceae	94	4	4.26
Myrtaceae	90	5	5.56
Chrysobalanaceae	60	1	1.67
Bruniaceae	57	1	1.75
Zamiaceae	45	5	11.11
Bignoniaceae	40	1	2.50
Droseraceae	33	2	6.06
Alliaceae	32	1	3.13
Tecophilaeaceae	16	4	25.00
Haemodoraceae	9	2	22.22
Bombaceae	7	2	28.86
Strelitziaceae	5	1	20.00
Kirkiaceae	5	1	20.00
Musaceae	4	2	50.00
Podocarpaceae	4	1	25.00
Caricaceae	2	1	50.00
Gunneraceae	1	1	100.00

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Table 3. Types of pollinators in African pollination papers

Pollinator category	Number of papers (JGR and BG combined)	Pollinator subcategory	Number of papers (JGR only)
Hymenoptera	131	Honeybees	25
		Oil-collecting bees	18
		Other bees	47
		Agaonid wasps	17
		Other wasps	8
Diptera	51	Long proboscid flies (Nemestrinidae and Tabanidae *sensu* Goldblatt & Manning	27
		Short-tongued flies	27
Coleoptera	32	Monkey beetles (Scarabaeidae, Rutelinae, Hopliini)	16
		Other beetles	10
Lepidoptera	41	Butterflies	24
		Hawkmoths (Sphingidae)	22
		Other moths	14
Birds	53		
Bats	16		
Non-flying mammals	18		
Wind	16		
Self	5		
Total	344		118

coverage is small. Central Africa, and Madagascar, which are important centres of biological diversity, have even less coverage.

Within South Africa a disproportionately large number of studies has been conducted in the Cape region (Fig. 4), which, despite being highly speciose, makes up a small fraction of South Africa's land area. This is the only region in Africa where pollination biology might be regarded as reasonably well studied. The synthesis report of pollination biology of this region (Rebelo, 1987a) is unique in the continent, not only for the wealth of information it contains about African pollination biology but also for placing this information in a global context. Rebelo (1987a), however makes the point that even in this region knowledge cannot be regarded as comprehensive. The Cape region of South Africa is quite distinct from the rest of the continent (Goldblatt and Manning, 2000) and with the exception of the afromontane/afroalpine archipelago, which has biogeographical affinities to the Cape (Goldblatt, 1978; Carbutt and Edwards, 2001), the relatively thorough understanding of pollination biology here is likely to have limited relevance elsewhere.

Africa is different

There has been much debate concerning differences between the ecology of northern hemisphere temperate, arctic and alpine systems and southern or tropical ecosystems. Pollination biology originated in Europe and it has been well investigated there, and in North America. Although during recent decades the field has increasingly been informed by tropical research (Rebelo, 1987a; Renner and Feil, 1993; Aizen and Feinsinger, 1994; Pinheiro-Machado *et al.*, 2002) understanding of

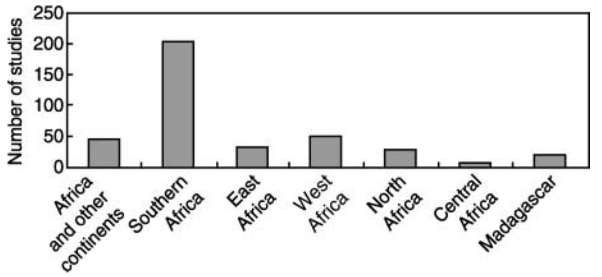

Fig. 3. Geographical areas and countries in which African pollination studies have been conducted

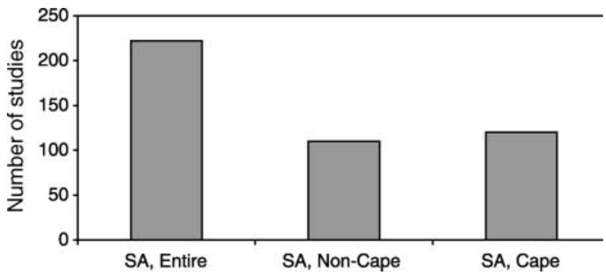

Fig. 4. Geographical focus of pollination studies within South Africa

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pollination biology within Africa is not at all comprehensive and hence the continent makes a much smaller contribution to the theoretical underpinnings of the field than should be the case. European and North America research therefore continues to underpin conceptual frameworks for pollination research globally, to a greater extent than is warranted. Theory based on studies conducted in the North temperate regions may be inadequate to explain systems in Africa (e.g. Stafford Smith, 1996; Illius and O'Conner, 1999), as many of the papers reviewed show that pollination biology in Africa differs substantially in certain aspects from that in the rest of the world, particularly Europe.

A number of unusual breeding systems have been noted in African plants. Some African *Eugenia* spp. (Myrtaceae) are morphologically androdioecious, but functionally dioecious. This is unusual for Myrtaceae, and different to *Eugenia* species found elsewhere (van Wyk and Lowry, 1988). *Canthium mundianum* (Rubiaceae) is morphologically gynodioecious but functionally dioecious (Balkwill *et al.*, 1996). A sterility barrier has been found between *Disa racemosa* and *Disa venosa*, which are sympatric. This is highly unusual for the family Orchidaceae (Johnson *et al.*, 1998). About 6.6% of the Cape flora (as defined by Rebelo, 1987a) is dioecious, a figure higher than that reported for other mainland temperate floras, particularly Mediterranean ones (Steiner, 1987).

African studies have contributed to the recognition of bats (e.g. Baker and Harris, 1959; Ayensu, 1974), in tropical ecosystems, and birds (e.g. Arroyo, 1981; Rebelo, 1987b) almost everywhere (except in Europe and northern Asia), as important pollinators. Unique pollination systems involving oil-collecting bees (Steiner and Whitehead, 1996; Steiner, 1999), long proboscid flies (Goldblatt and Manning, 1999; Manning and Goldblatt, 1997) and monkey beetles (Picker and Midgley, 1996; Goldblatt *et al.*, 2000, etc.) are known from South Africa. Monkey beetle pollination differs from the general beetle pollination syndrome (Proctor *et al.*, 1996a) in that visual attraction seems more important than odour; the beetles are particularly hairy and many species do little damage to the flowers. This pollinator group, unique to southern Africa, is believed to be one of the most important pollinator groups in the Cape region (Picker and Midgley, 1996). Bird-pollinated orchids elsewhere are thought to usually occur in dispersed populations which do not attract resident nectar-feeding birds; however, bird-pollinated African *Satyrium* spp. often form dense populations and do attract resident nectar-feeding birds (Johnson, 1996b).

Unusual diversity in pollination systems is a characteristic of *Disa*, *Satyrium*, *Erica*, *Gladiolus* and many other genera in the Cape flora (Johnson, 1996a). Johnson (1996a) suggests that variation in availability of pollinators in the Cape region led to adaptive shifts in pollination systems and this has contributed to high species diversity in these Cape genera. Johnson and Steiner (2003) compared level of specialization of pollination systems in the two most well studied families in temperate southern Africa (Orchidaceae and Iridaceae) and North America (Orchidaceae and Polemoniaceae) and found that southern African species displayed much higher levels of specialization to pollinators than those in North America. Orchid species, for instance, had a median of one pollinator species in southern Africa but five in North America.

Research needs

The pollination biology of the vast majority of African plant taxa remains un-investigated. A better understanding of pollination biology will enhance our understanding of population and community ecology and of agricultural systems, *inter alia*. Pollination biology can therefore make an important contribution to conservation of biodiversity and improvement of food security in Africa.

While there is a general lack of basic information on pollination relationships there is also a need for research that goes beyond simply documenting these. In particular there is a need for community level studies to identify sustainable management of pollinators for both agriculture and conservation. Important observations on pollination have been made during the course of systematic studies (e.g. Steiner, 1992; Manning *et al.*, 1999, etc.). Workers in fields other than pollination biology can thus make a significant contribution by making observations and collections of plants and flower visitors during the course of their work. Pollination biology also represents a wonderful opportunity for research by amateurs and this should be actively encouraged. Studies such as Goldblatt and Manning (1999) involved only 4–8 h of observation per species. Even purely observational studies will continue to remain valuable until a much more thorough understanding of pollination biology in Africa is reached.

There are still gaping inadequacies in our knowledge and understanding of pollination in Africa. The novelty of discoveries already made suggests that as further work is done in Africa, more differences between this continent and the rest of the world will be found and the overall conceptualization of pollination systems in different ecosystems may be better elaborated. Moreover, pollination research can make a substantial contribution to the improvement of food security and conservation in Africa.

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References

Aizen M. A. and Feinsinger P. (1994) Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology* 75, 330–351.

Arroyo M. T. K. (1981) Breeding systems and pollination biology in Leguminosae, pp. 723–769. In *Advances in Legume Systematics* (Edited by R. M. Polhill and P. H. Raven). Kew Royal Botanic Gardens, London.

Ayensu E. S. (1974) Plant and bat interactions in W. Africa. *Ann. Mo. Bot. Gard.* 61, 702–727.

Baker H. G. and Harris B. J. (1959) Bat-pollination of the silk-cotton tree, *Ceiba pentandra* (L.) Gaertn. (sensu lato), in Ghana. *J. W. Afr. Sci. Assoc.* 5, 1–9.

Balkwill K., Sebola J. R. and Robinson E. R. (1996) Sex expression in *Canthium mundianum* (Rubiaceae), pp. 650–655. In *The Biodiversity of African plants* (Edited by L. J. G. van der Maesen, X. M. Van der Burgt and J. M. van Medenbach de Rooy). Kluwer Academic Publishers, Dordrecht.

Beentje H. J., Adams B. and Davis S. D. (1994) Regional overview: Africa, pp. 101–264. In *Centres of Plant Diversity* Vol. I . IUCN Publications Unit, Cambridge.

Bogdan A. V. (1962) Grass pollination by bees in Kenya. *Proc. Linn. Soc. London* 173 (1), 57–173.

Buchmann S. L. and Nabhan G. P. (1996) *The Forgotten Pollinators*. Island Press, Washington D.C. 292 pp.

Cane, J. H. and Tepedino, V. J. (2001) Causes and extent of declines among native North American invertebrate pollinators: detection, evidence and consequences. Conservation Ecology 5, URL: http://www.ecologyandsociety.org/vol5/iss1/

Carbutt C. and Edwards T. (2001) Cape elements on high-altitude corridors and edaphic islands: historical aspects and preliminary phytogeography. *Syst. Geog.* 71, 1033–1061.

Crane E. and Walker P. (1984) *Pollination Directory for World Crops*. International Bee Research Association, London.

Delaplane K. S. and Mayer D. F. (2000) *Crop Pollination by Bees*. CABI Publishing, Wallingford. 344 pp.

Donaldson J. S. (2002) Pollination in agricultural landscapes. A South African perspective, pp. 97–104. In *Pollinating Bees—The Conservation Link Between Agriculture and Nature* (Edited by P. Kevan and V. L. Imperatriz-Fonseca). Brazilian Ministry of Environment, Brasília.

Donaldson J. S., Nänni I., Zachariades C. and Kemper J. (2002) Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa. *Conserv. Biol.* 16, 1267–1276.

El-Kassaby Y. A. and Reynolds S. (1990) Reproductive phenology, parental balance and supplemental mass pollination in a Sitka spruce seed orchard. *For. Ecol. Manage.* 31, 45–54.

Free J. B. (1996) *Insect Pollination of Crops*. Academic Press, London. 684 pp.

Ghazoul J. (2002) Flowers at the front line of invasion? *Ecol. Entomol.* 27, 638–640.

Goldblatt P. (1978) An analysis of the flora of southern Africa: its characteristics, relationships and origins. *Ann. Mo. Bot. Gard.* 65, 369–436.

Goldblatt P. and Manning J. C. (1999) The long proboscid fly pollination system in *Gladiolus* (Iridaceae). *Ann. Mo. Bot. Gard.* 86, 758–774.

Goldblatt P. and Manning J. C. (Eds) (2000) *Cape Plants: A Conspectus of the Cape Flora of South Africa*. National Botanical Institute of South Africa, Pretoria.

Goldblatt P., Bernhardt P. and Manning J. C. (2000a) Adaptive radiation of pollination mechanisms in *Ixia* (Iridaceae: Crocoideae). *Ann. Mo. Bot. Gard.* 87, 564–577.

Goldblatt P., Manning J. C. and Bernhardt P. (2000b) Adaptive radiation of pollination mechanisms in *Sparaxis* (Iridaceae: Ixioideae). *Adansonia* 22, 57–70.

Groom M. J. (2001) Consequences of subpopulation isolation for pollination, herbivory and population growth in *Clarkia concinna concinna* (Onagraceae). *Biol. Conserv.* 100, 55–63.

Guillaumet J. L. (1984) The vegetation: an extraordinary diversity, pp. 37–54. In *Madagascar* (Edited by A. Jolly, P. Oberlé and R. Albinac). Madagascar. Pergamon Press, Oxford.

Illius A. W. and O'Conner T. G. (1999) On the relevance of nonequilibrium concepts to arid and semi-arid grazing systems. *Ecol. Appl.* 9, 798–813.

Immelmann K. and Eardley C. (2000) Gathering of grass pollen by solitary bees (Halictidae, Lipotriches) in South Africa. *Mitt. Mus. Naturkunde Berl., Zool. Reihe.* 76 (2), 263–268.

Institute for Scientific Information (2000) *Science Citation Index*. Institute for Scientific Information, Philadelphia.

Johnson S. D. (1996a) Pollination, adaptation and speciation in the Cape flora of South Africa. *Taxon* 45, 59–66.

Johnson S. D. (1996b) Bird pollination in South African species of *Satyrium* (Orchidaceae). *Plant Syst. Evol.* 203, 91–98.

Johnson S. D. (1997a) Pollination ecotypes of *Satyrium hallackii* (Orchidaceae) in South Africa. *Bot. J. Linn. Soc.* 123, 225–235.

Johnson S. D. (1997b) Insect pollination and floral mechanisms in South African species of *Satyrium* (Orchidaceae). *Plant Syst. Evol.* 204, 195–206.

Johnson S. D. and Steiner K. E. (2003) Specialised pollination systems in southern Africa. *S. Afr. J. Sci.* 99, 345–348.

Johnson S. D., Linder H. P. and Steiner K. E. (1998) Phylogeny and radiation of pollination systems in *Disa* (Orchidaceae). *Am. J. Bot.* 85, 402–411.

Kearns C. A., Inouye D. W. and Waser N. M. (1998)

Endangered mutualisms: the conservation of plant–animal interactions. *Annu. Rev. Ecol. Syst.* 29, 83–112.

Kevan P. and Imperatriz-Fonseca V. L. (Eds) (2002) *Pollinating Bees: The Conservation Link Between Agriculture and Nature*. URL: http://eco.ib.usp.br/beelab/livro_polinizadores.htm. Brazilian Ministry of the Environment, Brasilia.

Kevan P. G. and Phillips T. P. (2001) The economic impacts of pollinator declines: an approach to assessing the consequences. *Conserv. Ecol.* 5 (1), 8 [online] URL: http://www.consecol.org/vol5/iss1/art8.

Kingdon J. (1989) *Island Africa: The Evolution of Africa's Rare Plants and Animals*. Princeton University Press, Princeton, New Jersey. 287 pp.

Knapp E. E., Goedde M. A. and Rice K. J. (2001) Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations. *Oecologia* 128, 48–55.

Knuth P. (1898–1905) *Handbuch der blütenbiologie, 1–3*. Engelmann, Leipzig.

Knuth P. (1906–1909) *Handbook of pollination biology, 1–3*. Transl. J. A. Davis. Clarendon Press, Oxford.

Lamont B. B., Klinkhamer P. G. L. and Witkowski E. T. F. (1993) Population fragmentation may reduce fertility to zero in *Banksia goodii*—a demonstration of the Allee effect. *Oecologia* 94, 446–450.

Leistner O. A. (Ed.) (2000) Seed plants of southern Africa: families and genera. *Strelitzia*. Vol. 10. National Botanical Institute, Pretoria.

Lennartsson T. (2002) Extinction thresholds and disrupted plant–pollinator interactions in fragmented plant populations. *Ecology* 83, 3060–3072.

Manning J. C. and Goldblatt P. (1997) The *Moegistorhynchus longirostris* (Diptera: Nemestrinidae) pollination guild: long-tubed flowers and a specialised long-proboscid fly pollination system in southern Africa. *Plant Syst. Evol.* 206, 51–69.

Manning J. C., Goldblatt P. and Winter P. J. D. (1999) Two new species of *Gladiolus* (Iridaceae: Ixioideae) from South Africa and notes on long-proboscid fly pollination in the genus. *Bothalia* 29, 217–223.

McGregor S. E. (1976) *Insect Pollination of Cultivated Crop Plants*. United States Department of Agriculture, Washington, D.C. 411 pp.

NISC, (2001) *African Studies Index*. Grahamstown, South Africa.

O'Toole C. (2002) Those other bees: changing the funding culture, pp. 37–40. In *Pollinating Bees—The Conservation Link Between Agriculture and Nature* (Edited by P. Kevan and V. L. Imperatriz-Fonseca). Brazilain Ministry of Environment, Brasília.

Owens J. N., Takaso T. and Runions C. J. (1998) Pollination in conifers. *Trends Plant Sci.* 3, 479–485.

Pankiw T. and Jay S. C. (1992) Aerially applied ultra-low-volume malathion effects on colonies of honey-bees (Hymenoptera: Apidae). *J. Econ. Entomol.* 85, 692–699.

Partap U. (2003) Research and development issues and opportunities in promoting conservation and sustainable use of pollinators. In *Proceedings, US State Department/ South African Agricultural Research Council Pollinator Workshop, at Mabula Lodge, Limpopo Province* May 2003

Picker M. D. and Midgley J. J. (1996) Pollination by monkey beetles (Coleoptera: Scarabaeidae: Hopliini): flower and colour preferences. *Afr. Entomol.* 4, 7–14.

Pinheiro-Machado C., Alves-dos-Santos I., Imperatriz-Fonseca V. L., Kleinert A. M. P. and Silveira F. A. (2002) Brazilian bee surveys: state of knowledge, conservation and sustainable use. In *Pollinating Bees: The Conservation Link Between Agriculture and Nature* (Edited by P. Kevan and V. L. Imperatriz-Fonseca). http://eco.ib.usp.br/beelab/livro 02 pinheiro_machado.pdf. Brazilian Ministry of the Environment, Brasilia Brazil.

Proctor M. C. F., Yeo P. F. and Lack A. J. (1996a) *The Natural History of Pollination*. Harper Collins Publishers, London.

Proctor M. C. F., Yeo P. F. and Lack A. J. (1996b) Pollination, community and environment. In *The Natural History of Pollination* (Edited by M. C. F. Proctor, P. F. Yeo and A. J. Lack). Harper Collins Publishers, London.

Rebelo A. G. (Ed.) (1987a) *A Preliminary Synthesis of Pollination Biology of the Cape Flora*. Council for Scientific and Industrial Research, Pretoria. 257 pp.

Rebelo A. G. (1987 b) Bird pollination in the Cape flora. In *A Preliminary Synthesis of Pollination Biology of the Cape flora* (Edited by A. G. Rebelo). Council for Scientific and Industrial Research, Pretoria. 257 pp.

Renner S. S. and Feil J. P. (1993) Pollinators of tropical dioecious angiosperms. *Am. J. Bot.* 80, 1100–1107.

Richardson D. M., Allsopp N. D., Antonio C. M., Milton S. J. and Rejmánek M. (2000) Plant invasions–the role of mutualisms. *Biol. Rev.* 75, 65–93.

Roubik D. (Ed.) (1995) *Pollination of Cultivated Plants in the Tropics. FAO Agricultural Services Bulletin, 118*. 196 pp.

Stafford Smith M. (1996) Management of rangelands: paradigms at their limits, pp. 325–357. In *The Ecology and Management of Grazing Systems*. (Edited by J. Hodgson and A. W. Illius). CAB International, Wallingford.

Steiner K. E. (1987) Breeding systems in the Cape flora, pp. 22–51. In *A Preliminary synthesis of Pollination Biology of the Cape Flora* (Edited by A. G. Rebelo). Council for Scientific and Industrial Research, Pretoria. 257 pp.

Steiner K. E. (1992) Two new *Diascia* species (Scrophulariaceae) from the Little Karoo. *S. Afr. J. Bot.* 58, 39–47.

Steiner K. E. (1999) A new species of *Diascia* (Scrophulariaceae) from the Eastern Cape (South Africa) with notes on other members of the genus in that region. *S. Afr. J. Bot.* 65, 223–231.

Steiner K. E. and Whitehead V. B. (1996) The consequences of specialisation for pollination in a rare South African shrub, *Ixianthes retzioides* (Scropulariaceae). *Plant Syst. Evol.* 201, 131–138.

Stone G. N., Willmer P. G. and Rowe J. A. (1998)

Partitioning of pollinators during flowering in an African *Acacia* community. *Ecology* 79, 2808–2827.
Stork A. C. and Le Brun J. P. (1997) *Ènumeration des Plantes à Fleurs d'Afrique Tropicale* Volume IV Gamopétales: Ericaceae à Lamiaceae. Ville de Genève, Geneva. 712 pp.
Thomson J. D. (2001) Using pollination deficits to infer pollinator declines: Can theory guide us? *Conserv. Ecol.* 5 (1), 6 [online] URL: http://www.consecol.org/vol5/iss1/art6.
Vogel S. (1954) Blütenbiologische Typen als Elemente der Sippengliederung, dargestellt anhand der Flora Südafrikas. *Bot. Studien I. Fischer, Jena.*, 358 pp.
Westerkamp C. and Gottsberger G. (2002) The costly crop pollination crisis, pp. 51–56. In *Pollinating Bees—The Conservation Link Between Agriculture and Nature* (Edited by P. Kevan and V. L. Imperatriz-Fonseca). Brasilian Ministry of Environment, Brasília.
Wilcock C. and Neiland R. (2002) Pollination failure in plants: why it happens and when it matters. *Trends Plant Sci.* 7, 270–277.
Williams I. H. (2002) Insect pollination and crop production: A European perspective, pp. 59–65. In *Pollinating Bees—The Conservation Link Between Agriculture and Nature* (Edited by P. Kevan and V. L. Imperatriz-Fonseca). Brasilian Ministry of Environment, Brasília.
van Wyk A. E. and Lowrey T. K. (1988) Studies on the reproductive biology of *Eugenia* L (Myrtaceae) in southern Africa. *Monographs in Systematic Botany, Missouri Botanical Garden* 25, 279–293.

Appendix 1. List of publications on pollination biology in Africa

Ahmed H. M. H., Siddig M. A. and El Sarrag M. S. A. (1989) Honeybee pollination of some cultivated crops in Sudan, pp. 100–108. In *Proceedings 4th Conference on Agriculture* in Tropical Climates, Cairo. London, International Bee Research Association.
Allan P. (1963) Pollination of pawpaws. *Fmg. S. Afr.* 81, 1–3.
Amoako J. and Yeboah-Gyan K. (1991) Insect pollination of three solanaceous vegetable crops in Ghana with special reference to the role of African honey bee (*Apis mellifera adansonii*) for fruit set. The 6th International Symposium on Pollination, Tilburg, The Netherlands, August 1990. *Acta Horticultura* 288, 255–259.
Armbruster W. S. (1986) Reproductive interaction between sympatric *Dalechampia* species: are natural assemblages "random" or organized? *Ecology* 67, 522–533.
Armbruster W. S. (1992) Phylogeny and the evolution of plant–animal interactions. *BioScience* 42, 12–20.
Armbruster W. S. and Mziray W. R. (1987) Pollination and herbivore ecology of an African *Dalechampia* (Euphorbiaceae): comparisons with new world species. *Biotropica* 19, 64–73.
Armbruster W. S., Mziray M. E., Hines J. F., Mahunnah R. L. A. and Munyenyembe P. (1993) Evolution and Pollination of Madagascan and African *Dalechampia*. *Natl. Geog. Res. Exploration* 9, 460–474.
Armbruster W. S. and Steiner K. E. (1992) Pollination ecology of four *Dalechampia* species (Euphorbiaceae) in northern Natal, South Africa. *Am. J. Bot.* 79, 306–313
Arroyo, M. T. K. (1981) Breeding systems and pollination biology in Leguminosae, pp. 723–769. In *Advances in Legume Systematics* (Edited by R. M. Polhill and P. H. Raven). Kew Royal Botanic Gardens, London.
Ayensu, E. S. (1974) Plant and bat interactions in West Africa. *Ann. Mo. Bot. Gard.* 61, 702–727.
Baijnath H. and Naicker S. (1989) Developmental anatomy of *Ficus ingens* syconia in relation to its host wasp faunula. *S. Afr. J. Bot.* 55, 409–421.
Baijnath H. and Ramcharan S. (1983) Aspects of pollination and floral development in *Ficus capensis* Thunb. (Moraceae) *Bothalia* 14, 883–888.
Baijnath H. and Ramcharan S. (1988) Reproductive biology and chalcid symbiosis in *Ficus burtt-davyi* (Moraceae) *Monographs in systematic botany, Missouri Botanical Garden* 25, 227–235.
Baijnath H., Naicker S. and Ramcharan S. (1983) Aspects of pollination in some South African monoecious figs (*Ficus* spp., Moraceae). *S. Afr. J. Bot.* 2, 247.
Baker H. G. (1958) Studies in the reproductive biology of West African Rubiaceae. *J. W. Afr. Sci. Assoc.* 4, 9–24.
Baker H. G. (1961) The adaptation of flowering plants to nocturnal and crepuscular pollinators. *Q. Rev. Biol.* 36, 64–73.
Baker H. G. (1976) "Mistake" pollination as a reproductive system with special reference to the Caricaceae, pp. 161–169. In *Tropical trees: variation, breeding and conservation* (Edited by J. Burley B. T. Styles). Academic Press, London.
Baker I. and Baker H. G. (1982) Some chemical constituents of floral nectars of *Erythrina* in relation to pollinators and systematics. *Allertonia* 3, 25–37.
Baker H. G. and Harris B. J. (1959) Bat pollination of the silk cotton tree, *Ceiba pentandra* (l.) Gaertn (sensu lato) in Ghana. *J. W. Afr. Sci. Assoc.* 5, 1–9.
Baker H. G. and Harris B. J. (1957) The pollination of *Parkia* by bats and its attendant evolutionary problems. *Evolution* 11, 449–460.
Balkwill M. J. and Balkwill K. (1999) Floral polymorphism in a forest species, *Pseuderanthum subviscosum* (C. B. Clarke) Stapf (Acanthaceae). In *African plants: biodiversity, taxonomy and uses* (Edited by J. Timberlake and S. Kativu). Royal Botanic Gardens, Kew.
Balkwill M. J., Balkwill K. and Vincent P. L. D. (1990) Systematic studies in the Acanthaceae: A new species of *Barleria* from Natal. *S. Afr. J. Bot.* 56, 571–576.
Balkwill K. and McCallum D. A. (1999) A review of African forest Acanthaceae, pp. 11–21. In *African Plants: Biodiversity, Taxonomy and Uses* (Edited by J. Timberlake and S. Kativu). Royal Botanic Gardens, Kew.
Balkwill K., Sebola J. R. and Robinson E. R. (1996)

https://doi.org/10.1079/IJT20045 Published online by Cambridge University Press

Sex expression in *Canthium mundianum* (Rubiaceae), pp. 650–655. In *The Biodiversity of African Plants* (Edited by L. J. G. van der Maesen, X. M. Van der Burgt and J. M. van Medenbach de Rooy). Kluwer Academic Publishers, Dordrecht.

Balls W. L. (1929) The natural crossing of cotton flowers in Egypt. *Bull. Minist. Agric. Egypt* 89.

Baum D. A. (1995) The comparative pollination and floral biology of baobabs (*Adansonia* Bombaceae) *Ann. Mo. Bot. Gard.* 82, 322–348.

Bayer M. B. (1978) Pollination in asclepiads. *Veld and Flora* 64, 21–23.

Bigger M. (1960) *Selenothrips rubrocinctus* (Giard) and the floral biology of cashew in Tanganyika. *E. Afr. Agric. J.* 25, 229–234.

Boitreau P. and Allorge L. (1977) Morphologie et biologie florales des Apocynacees. *Adansonia* 2(17), 305–326.

Bond W. J. (1994) Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 344, 83–90.

Bond W. J., Midgley J. and Vlok, J. (1988) When is an island not an island? Insular effects and their causes in fynbos shrublands. *Oecologia* 77, 515–521.

Bouriquet G. (1954) Le vanillier et la vanille, pp. 441–453. In *Encyclopedie Biologique 66*. Paris, Paul Lechavalier.

Brantjes N. B. M. and de Vos O. C. (1981) The explosive release of pollen in flowers of *Hyptis* (Lamiaceae). *New Phytol.* 87, 425–30.

Brew A. H. (1987) The effect of colours and specific features of floral parts on the pollination of cocoa by ceratopogonid midges in Ghana. In *Proceedings of the Tenth International Cocoa Research Conference, Santo Domingo, Dominican Republic* 17–23 May 1988.

Brew A. H. (1988) Cocoa pod husk as a breeding substrate for *Forcipomyia* midges and related species which pollinate cocoa in Ghana. *Cocoa Growers' Bulletin* 40, 40–42.

Buys M. H. and van der Walt J. J. A. (1996) A new species of *Lobostemon* section Grandiflora (Boraginaceae) from South Africa. *S. Afr. J. Bot.* 62, 31–35.

Carpenter F. L. (1983) Pollination energetics in avian communities: simple concepts and complex realities, pp. 215–234. In *Handbook of Experimental Pollination Biology* (Edited by C. E. Jones and R. J. Little). Van Nostrand Reinhold, New York.

Chandler M. T. (1976) Reducing pesticide hazards to honeybees in tropical East Africa. *Pans* 22, 35–42.

Chandler S. E. (1956) Botanical aspects of pyrethrum III. The natural history of the secretory organs: the pyrethrins content of the fertile achenes. *Pyrethrum Post* 4, 10–15.

Chenon R. D. de (1982) Entomophil pollination of oil palm in West Africa – preliminary research, pp. 291–323. In *The Oil Palm in the Eighties, A Report of the Proceedings of the International Conference on Oil Palm in the Eighties. Kuala Lumpar, 17–20 June 1981. Vol. 1* (Edited by E. Pushparajah and Chew Poh Soon). Society of Planters, Kuala Lumpar.

Coe M. J., McWilliam N. C., Stone G. N. and Packer M. J. (Eds) (1999) *Mkomazi: the Ecology, Biodiversity and Conservation of a Tanzanian Savanna*. Royal Geographical Society (with The Institute of British Geographers), London.

Coetzee J. H. and Giliomee J. H. (1985) Insects in association with the inflorescences of *Protea repens* (L.) (Proteaceae) and their role in pollination. *J. Ent. Soc. Sth. Afr.* 48, 303–314.

Collins B. G. (1983) Pollination of *Mimetes hirtus* (Proteaceae) by Cape sugarbirds and orange-breasted sunbirds. *S. Afr. J. Bot.* 49, 125–142.

Collins B. G. and Rebelo T. (1987) Pollination biology of the Proteaceae in Australia and Southern Africa. *Aust. J. Ecol.* 12, 387–421.

Compton S. G. (1990) A collapse of host specificity in some African fig wasps. *S. Afr. J. Sci.* 86, 39–40.

Compton S. G. and Nefdt R. J. C. (1990) The figs and fig wasps of *Ficus burtt-davyi*, pp. 441–450. In *Proceedings of the twelfth plenary meeting of AETFAT.*

Cope F. W. (1940b) Agents of pollination in cacao. *Rep. Cacao Res.* 9, 13–19.

Correll D. S. (1953) Vanilla, its botany, history, and culture and economic importance, *Econ. Bot.* 7, 291–358.

Cowling R. M. and Mitchell D. T. (1981) Sugar composition, total nitrogen and accumulation of C-14, assimilates in floral nectaries of *Protea* species. *S. Afr. J. Bot.* 47, 743–750.

Danforth B. N., Eardley C. D., Walker K. and Packer L. (2001) Report on First Trip to South Africa on National Geographic Society Grant: Historical Biogeography and Sociality of African Halictine Bees (unpublished report).

de Lange J. H. (1989) Significance of autoclaving-induced toxicity from and hydrolysis of carbohydrates in *in vitro* studies of pollination germination and growth. *S. Afr. J. Bot.* 55, 1–5.

de Lange J. H. and Vincent A. P. (1988) Studies on *Citrus* pollination using gamma-irradiated pollen. *S. Afr. J. Bot.* 54, 257–264.

de Lange J. H., Boucher C. and van der Walt J. J. A. (1993) Autecological studies on *Audouinia capitata* (Bruniaceae) III. Pollination biology. *S. Afr. J. Bot.* 59, 135–144.

Doku E. V. (1968) Flowering, pollination and pod formation in bambara groundnut (*Voandzeia subterranean*) in Ghana. *Expl. Agric.* 4, 41–48 + 3 plates.

Doku E. V. and Karikari S. K. (1971) The role of ants in pollination and pod production of bambara groundnut. *Econ. Bot.* 25, 357–362.

Dowsett-Lemaire F. (1989) Food plants and the annual cycle in a montane community of sunbirds (*Nectarinia* spp.) in northern Malawi. *Tauraco* 1, 167–185.

Dressler R. L. (1981) *The Orchids, Natural History and Classification*. Harvard University Press, Cambridge, Mass.

Dulberger R. and Ornduff R. (1980) Floral morphology and reproductive biology of four species of *Cyanella* (Tecophilaeaceae). *New Phytol.* 86, 45–56.

du Toit A. P. (1988) The pollination ecology of commercial sunflower (*Helianthus annuus* L.) in South Africa with

special reference to the honeybee (*Apis mellifera* L.). MSc thesis, University of Pretoria, South Africa.
du Toit A. P. and Coetzer L. A. (1991) Difference in potential attractiveness of bees of seventeen South African sunflower (*Helianthus annuus*) cultivars. The 6th International Symposium on Pollination, Tilburg, The Netherlands, August 1990. *Acta Horticultura* 288, 288–293.
du Toit J. T. (1990) Giraffe feeding on *Acacia* flowers: predation or pollination? *Afr. J. Ecol.* 28, 63–68.
Eardley C. D. and Mansell M. W. (No date) The natural occurrence of insect pollinators in a mango orchard: final report. *South African Mango Grower's Association Yearbook* 15, 89–91.
El-Berry A. A., Moustafa M. A., Abdel-Gawaad A. A. and El-Bialey S. (1974) Pollinators other than honey bees visiting certain vegetable plants in Egypt. *Z. Angew. Ent.* 77, 106–110.
El-Berry A. A., Gawaad A. A. A., Moustafa M. A. F. and El-Gayar F. H. (1974) Pollinators other than honey bees visiting certain medicinal plants in Egypt. *Z. Angew. Ent.* 76, 113–119.
El-Borollosy F. M., Mohamed M. I. and Allam H. M. (1975) Insect pollinators of clover in the new reclaimed land of Quesna, Egypt. *Bull. Soc. Ent. Egypte* 59, 161–168.
Entwhistle H. (1956) Cacao pollination. *Proceedings Cacao Breeding Conference, 19–21*. West African Cacao Research Institute, Tafo.
Evans M. S. (1895) The fertilisation of *Loranthus kraussianus* and *L. dregei*. *Nature* 51, 235–236.
Faden R. B. (1983) Isolating mechanisms among five sympatric species of *Aneilema* R. Br. (Commelinaceae) in Kenya. *Bothalia* 14, 997–1002.
Feehan J. (1985) Explosive flower opening in ornithophily: a study of pollination mechanisms in some Central African Loranthaceae. *Bot. J. Linn. Soc.* 90, 129–144.
Ferguson I. K. and Skvarla J. J. (1982) Pollen morphology in relation to pollinators in Papilonoideae (Leguminosae). *Bot. J. Linn. Soc.* 84, 183–193.
Franssen-Verheijen M. A. and Willemse M. T. M. (1993) Micropylar exudate in *Gasteria* (Aloaceae) and its possible function in pollen tube growth. *Am. J. Bot.* 80, 253–262.
Frost S. K. and Frost P. G. H. (1981) Sunbird pollination of *Strelitzia nicolai*. *Oecologia* 49, 379–384.
Galil J., Dulberger R. and Rosen D. (1970) The effects of *Sycophaga sycomori* L. on the structure and development of the syconia in *Ficus sycomorus* L. *New Phytol.* 69, 103–111.
Galil J. and Eisikovitch D. (1968) On the pollination ecology of *Ficus sycomorus* in East Africa. *Ecology* 49, 259–269.
Galil J. and Eisikowitch D. (1974) Further studies on pollination ecology in *Ficus sycomorus*. II. Pocket filling and emptying by *Ceratosolen arabicus* Mayr. *New Phytol.* 73, 515–528.
Gater B. A. R. (1925) Insects of African oil palms. *Malay Agric. J.* 13, 250–256.
Gess S. K. and Gess F. W. (1989) Flower visiting by masarid wasps in southern Africa (Hymenoptera: Vespoideae: Masaridae). *Ann. Cape Prov. Mus. (Nat. Hist.)* 18, 95–134.
Gess F. W. and Gess S. K. (1993) Effects of increasing land utilization on species representation and diversity of aculeate wasps and bees in the semi-arid areas of Southern Africa, pp. 83–114. In *Hymenoptera and Biodiversity* (Edited by J. LaSalle and I. D. Gauld). CAB International, Oxon (UK).
Gibbons R. W. and Tatterfield J. R. (1969) Out-crossing trials with groundnuts (*Arachis hypogaea* L.) *Rhodesia J. Agric. Res.* 7, 71–75.
Gill F. B. and Wolf L. L. (1975) Foraging strategies and energetics of east African sunbirds at mistletoe flowers. *Am. Nat.* 109, 491–510.
Gill F. B. and Wolf L. L. (1977) Non-random foraging by sunbirds in a patchy environment. *Ecology* 58, 1284–1296.
Gill F. B. and Wolf L. L. (1978) Comparative foraging efficiencies of some montane sunbirds in Kenya. *Condor* 80, 391–400.
Glendinning D. R. (1958) Natural pollination. *Rep. W. Afr. Cocoa Res. Inst. (1957–1958)* 50–51.
Goldblatt P. (1979) Biology and systematics of *Galaxia* (Iridaceaea). *S. Afr. J. Bot.* 45, 385–423.
Goldblatt P. (1981) Systematics and biology of *Homeria* (Iridaceae). *Ann. Mo. Bot. Gard.* 68, 413–503.
Goldblatt P. (1986) Convergent evolution of the *Homeria* flower type in six new species of *Moraea* (Iridaceae-Irideae) in southern Africa. *Ann. Mo. Bot. Gard.* 73, 106–116.
Goldblatt P. (1989) The genus *Watsonia*: a systematic monograph. pp. 19–23. National Botanical Gardens, Pretoria.
Goldblatt P. (1990) Status of the southern African *Anapalina* and *Antholyza* (Iridaceae) genera, based solely on characters for bird pollination, and a new species of *Tritoniopsis. S. Afr. J. Bot.* 56, 577–582.
Goldblatt P. (1991) An overview of the systematics, phylogeny and biology of the African Iridaceae. *Contr. Bolus Herb.* 13, 1–74.
Goldblatt P. (1996a) The *Moraea*s of southern Africa: a systematic monograph of the genus in South Africa, Lesotho, Swaziland, Transkei, Botswana, Namibia and Zimbabwe, pp. 11–14. National Botanical Gardens, Pretoria.
Goldblatt P. (1996b) *Gladiolus* in Tropical Africa: Systematics, biology and evolution, pp. 43–52. Timber Press, Portland, Oregon.
Goldblatt P. and Bernhardt P. (1990) Pollination biology of *Nivenia* (Iridaceae) and the presence of heterostylous self incompatibility. *Israel J. Bot.* 39, 93–111.
Goldblatt P. and Bernhardt P. (1999) Pollination of *Moraea* species (Iridaceae) with a staminal column. *Ann. Mo. Bot. Gard.* 86, 47–56.
Goldblatt P. and Manning J. C. (1997) New species of *Aristea* (Iridaceae) from South Africa and notes on the taxonomy and pollination biology of section *Pseudaristea*. *Novon* 7, 137–144.
Goldblatt P. and Manning J. C. (1998) *Gladiolus* in

https://doi.org/10.1079/IJT20045 Published online by Cambridge University Press

southern Africa, pp. 24–32. Fernwood Press, Vlaeberg.

Goldblatt P. and Manning J. C. (1999) The long proboscid fly pollination system in *Gladiolus* (Iridaceae). *Ann. Mo. Bot. Gard.* 86, 758–774.

Goldblatt P., Bernhardt P. and Manning J. C. (1989) Notes on the pollination mechanisms of *Moraea inclinata* and *M. brevistyla* (Iridaceae) *Plant Syst. Evol.* 163, 201–209.

Goldblatt P., Bernhardt P. and Manning J. C. (1998) Pollination of petaloid geophytes by monkey beetles (Scarabaeidae: Rutelinae: Hopliini) in southern Africa. *Ann. Mo. Bot. Gard.* 85, 215–230.

Goldblatt P., Bernhardt P. and Manning J. C. (2000) Adaptive radiation of pollination mechanisms in *Ixia* (Iridaceae: Crocoideae). *Ann. Mo. Bot. Gard.* 87, 564–577.

Goldblatt P., Manning J. C. and Bernhardt P. (1995) Pollination in *Lapeirousia* subgenus *Lapeirousia* (Iridaceae: Ixioideae). *Ann. Mo. Bot. Gard.* 82, 517–534.

Goldblatt P., Manning J. C. and Bernhardt P. (1998) Adaptive radiation of bee-pollinated *Gladiolus* species (Iridaceae) in southern Africa. *Ann. Mo. Bot. Gard.* 85, 492–517.

Goldblatt P., Manning J. C. and Bernhardt P. (1999) Evidence of bird pollination in Iridaceae of southern Africa. *Adansonia* 21, 25–40.

Goldblatt P., Manning J. C. and Bernhardt P. (2000) Adaptive radiation of pollination mechanisms in *Sparaxis* (Iridaceae: Ixioideae). *Adansonia* 22, 57–70.

Goldingay R. L., Carthew S. M. and Whelan R. J. (1991) The importance of non-flying mammals in pollination. *Oikos* 61, 79–87.

Greathead D. J. (1983) The multi-million dollar weevil that pollinates oil palms. *Antenna* 7(3), 105–107.

Greenway P. J. and Wallace M. M. (1953) The pawpaw, its botany, cultivation, diseases and chemistry. Pamphl. Dep. Agric. Tanganyika 52.

Grey-Wilson C. (1980) Morphology, pollination and pollinators, ecology, phytogeography, hybridisation, keys, and a systematic treatment of all African species with a note on collecting and cultivation, pp. 25–26. In *Impatiens of Africa.* Balkema, Rotterdam.

Guillarmod A. J., Jubb R. A. and Skead C. J. (1979) Field studies of six southern African species of *Erythrina*. *Ann. Mo. Bot. Gard.* 66, 521–527.

Hagerup O. (1932) On pollination in the extremely hot air at Timbuctu. *Dansk Botansk. Arjkiv* 8(1), 1–20.

Hall A. V. (1987) Gene flow in plant populations, pp. 134–155. In *A Preliminary Synthesis of Pollination Biology of the Cape Flora* (Edited by A. G. Rebelo). Council for Scientific and Industrial Research, Pretoria.

Harris B. J. and Baker H. G. (1958) Pollination in *Kigelia africana* Benth. *J. W. Afr. Sci. Assoc.* 4, 25–30.

Harris B. J. and Baker H. G. (1959) Pollination of flowers by bats in Ghana. *Nigeria Field* 24, 151–159.

Hassanein M. H. and Ibrahim M. M. (1959) Studies on the importance of insects, especially honeybee, in pollination of citrus in Egypt. *Agric. Res. Rev., Cairo* 37, 390–409.

Hassanein M. H. (1953) Studies on the effect of pollinating insects, especially the honeybee on the seed yield of clover in Egypt. *Bull. Soc. Fouad Im. Ent.* 37, 337–344.

Hassanein M. H. (1955) The value of pollinating insects to flax seed production in Egypt. *Ann. Agric. Sci. Univ. A'in Shams,* 773–784.

Hassanein M. H. and El Banby M. A. (1956) Studies on the ability of the Egyptian honeybee on carrying nectar & pollen. *Ann. Agric. Sci. Fac. Agric. A'in Shams* 23–26.

Hattingh V. and Giliomee J. H. (1989) Pollination of certain *Leucadendron* species (Proteaceae). *S. Afr. J. Bot.* 55, 387–393.

Hemsley A. J. and Ferguson I. K. (1985) Pollen morphology of the genus *Erythrina* (Leguminosae: Papilionoideae) in relation to floral structure and pollinators. *Ann. Mo. Bot. Gard.* 72, 570–590.

Henderson A. (1986) A review of pollination studies in the Palmae. *Bot. Rev.* 52, 221–259.

Hill D. S. (1967) Figs (*Ficus* spp) and fig-wasps (Chalcidoidea). *J. Nat. Hist.* 1, 413–434.

Hoffman M. T. (1988) The pollination ecology of *Aloe ferox* Mill. *S. Afr. J. Bot.* 54, 345–350.

Honig M. A., Linder H. P. and Bond W. J. (1992) Efficacy of wind pollination: pollen load size and natural microgametophyte populations in windpollinated *Staberoha banksii* (Restionaceae). *Am. J. Bot.* 79, 443–448.

Hopkins H. C. (1983) The taxonomy, reproductive biology and economic potential of *Parkia* (Leguminosae: Mimosoideae) in Africa and Madagascar. *Bot. J. Linn. Soc.* 87, 135–167.

Hopkins H. C. and White F. (1984) The ecology and chorology of *Parkia* in Africa. *Bull. Jard. Bot. Nationale de Belg.* 54, 235–66.

Horn W. (1962a) Breeding research on South African plants: II. Fertility of Proteaceae. *J. S. Afr. Bot.* 28, 259–268.

Horn W. (1962b) Breeding research on South African plants: III. Intra- and interspecific compatibility in *Ixia* L., *Sparaxis* Ker., *Watsonia* Mill. and *Zantedeschia* Spreng. *J. S. Afr. Bot.* 28, 269–277.

Hussein M. H. and Abdel-Aal S. A. (1982) Wild and honey bees as pollinators of ten plants in the Assiut area, Egypt. *Z. Angew. Ent.* 93(4), 342–346.

Ibrahim A. G. and Hussein A. M. (1987) Role of insects in the pollination of cocoa flowers. *Pertanika* 10, 103–106.

Immelman K. (1984) Simaroubaceae: flowering in *Kirkia wilmsii* Engl. *Bothalia* 15, 151–152.

Janzen D. H. (1979) How to be a fig. *Annu. Rev. Ecol. Syst.* 10, 13–51.

Jay S. C. (1974) Nectar and pollen collection by honeybees from coconut flowers. *Bee Wld* 55, 105–111.

Johnson C. F. and Phillipson P. B. (1999) Reproductive biology of *Tetradenia* Benth. (Lamiaceae), pp. 97–104. In *African Plants: Biodiversity, Taxonomy and Uses* (Edited by J. Timberlake and S. Kativu). Royal Botanic Gardens, Kew.

Johnson C. T. and Weitz F. M. (1991) A re-evaluation of *Nylandtia* (Polygalaceae). *S. Afr. J. Bot.* 57, 229–233.

Johnson L. A. S. and Briggs B. G. (1975) On the Proteaceae – the evolution and classification of a southern family. *Bot. J. Linn. Soc.* 70, 83–182.

Johnson S. D. (1992a) Plant animal relationships, pp. 175–205. In *The Ecology of Fynbos: Nutrients, Fire and Diversity* (Edited by R. M. Cowling). Oxford University Press, Cape Town.

Johnson S. D. (1992b) Pollination of *Disa filicornis* (Orchidaceae) through deception of mason-bees. *S. Afr. J. Bot* 58, 541–542.

Johnson S. D. (1994) Evidence for Batesian mimicry in a butterfly-pollinated orchid. *Biol. J. Linn. Soc.* 53, 91–104.

Johnson S. D. (1995) Observation of hawkmoth pollination in the South African orchid *Disa cooperi*. *Nordic J. Bot.* 15, 121–125.

Johnson S. D. (1996a) Pollination, adaptation and speciation in the Cape flora of South Africa. *Taxon* 45, 59–66.

Johnson S. D. (1996b) Bird pollination in South African species of *Satyrium* (Orchidaceae) *Plant Syst. Evol.* 203, 91–98.

Johnson S. D. (1997a) Pollination ecotypes of *Satyrium hallackii* (Orchidaceae) in South Africa. *Bot. J. Linn. Soc.* 123, 225–235.

Johnson S. D. (1997b) Insect pollination and floral mechanisms in South African species of *Satyrium* (Orchidaceae). *Plant Syst. Evol.* 204, 195–206.

Johnson S. D. and Bond W. J. (1992) Habitat dependent pollination success in a Cape orchid. *Oecologia* 91, 455–456.

Johnson S. D. and Bond W. J. (1994) Red flowers and butterfly pollination in the fynbos of South Africa, pp. 137–148. In *Plant–Animal Interactions in Mediterranean Ecosystems* (Edited by M. Arianoutsou and R. Groves). Kluwer Academic Press, Dordrecht.

Johnson S. D. and Bond W. J. (1997) Evidence for widespread pollen limitation of fruiting success in Cape wildflowers. *Oecologia* 109, 530–534.

Johnson S. D. and Liltved W. R. (1996) Hawkmoth pollination of *Bonatea speciosa* (Orchidaceae) in a South Africa coastal forest. *Nordic J. Bot.* 17, 5–10.

Johnson S. D. and Midgley J. J. (1997) Fly pollination of *Gorteria diffusa* (Asteraceae), and a possible mimetic function for dark spots on the capitulum. *Am. J. Bot.* 84, 429–436.

Johnson S. D. and Steiner K. E. (1994) Efficient pollination of the mass flowering Cape orchid *Disa obtusa* Lindl. (Orchidaceae) by *Bibio turneri* Edwards (Diptera: Bibionidae). *Afr. Entomol.* 2, 64–66.

Johnson S. D. and Steiner K. E. (1995) Long proboscid fly pollination of two orchids in the Cape Drakensberg Mountains. *Plant Syst. Evol.* 195, 169–175.

Johnson S. D. and Steiner K. E. (1997) Long tongued fly pollination and evolution of floral spur length in *Disa draconis* complex (Orchidaceae) *Evolution* 51, 45–53.

Johnson S. D. and Steiner K. E. (1999) Pollination, pp. 34–39. In *Orchids of Southern Africa* (Edited by H. P. Linder and H. Kurzweil). A. A. Balkema, Rotterdam.

Johnson S. D., Steiner K. E. and Kurzweil H. (1994) Auto-pollination in *Disa* species (Orchidaceae) of the Cape mountain cloud-zone. *Lindleyana* 9, 3–6.

Johnson S. D., Ellis A., Carrick P., Swift A., Horner N., Janse van Rensburg S. and Bond W. J. (1993) Moth pollination and rhythms of advertisement and reward in *Crassula fascicularis* (Crassulaceae). *S. Afr. J. Bot.* 59, 511–513.

Johnson S. D., Linder H. P. and Steiner K. E. (1998) Phylogeny and radiation of pollination systems in *Disa* (Orchidaceae). *Am. J. Bot.* 85, 402–411.

Johnson S. D., Steiner K. E., Whitehead V. B. and Vogelpoel L. (1998) Pollination ecology and maintenance of species integrity in co-occurring *Disa racemosa* L.f. and *Disa venosa* Sw. (Orchidaceae) in South Africa. *Ann. Mo. Bot. Gard.* 85, 231–241.

Kaufmann T. (1973) Preliminary observations on cecidomyiid midge and its role as a cocoa pollinator in Ghana. *Ghana J. Agric. Sci.* 6, 193–198.

Kaufmann T. (1974) Pollination, pp. 90–94. In Annual Report 1972–1973. *Cocoa Research Institute*. Council for Scientific and Industrial Research, Ghana.

Kaufmann T. (1975a) Cocoa pollination by males of *Forcipomyia squamipennis* (Diptera: Ceratopogonidae) in Ghana. *Trop. Agric.* 52, 71–74.

Kaufmann T. (1975b) An efficient, new cocoa pollinator, *Lasioglossum* sp. (Hymenoptera: Halicitidae) in Ghana, West Africa. *Turrialba* 25, 90–91.

Kenrick J. and Knox R. B. (1982) Function of the polyad in reproduction of *Acacia*. *Ann. of Bot.* 50, 721–727.

Kevan P. G., Hussein M. Y., Hussey N. and Wahid M. B. (1986) Modeling the use of *Elaeidobius kamerunicus* for pollination of oil palm. *Planter* 62, 89–99.

Khaemba B. M. (1985) Studies of sunflower pollination by the honeybee *Apis mellifera* L. (Apoidea: Hymenoptera) and the damage caused by the African bollworm *Heliothis armigera* Hb (Noctuidae: Lepidoptera) in Kenya. *Proceedings of the Third International Conference of Apiculture in Tropical Climates.*

Kinnaird M. (1992) Phenology of flowering and fruiting of an East African riverine forest ecosystem. *Biotropica* 24, 87–94.

Koutnik D. (1987) Wind pollination in the Cape flora, pp. 126–133. In *A Preliminary Synthesis of Pollination Biology of the Cape Flora* (Edited by A. G. Rebelo). Council for Scientific and Industrial Research, Pretoria.

Kress W. J., Schatz G. E., Andrianifahanana M. and Morland H. S. (1994) Pollination of *Ravenala madagascariensis* (Strelitziaceae) by lemurs in Madagascar: evidence for an archaic coevolutionary system? *Am. J. Bot.* 81, 542–551.

Kroll U. (1961) The influence of fertilization on the production of pyrethrum flower. *Pyrethrum Post* 6, 19–21.

Kunze H. (1990) Structure and function in asclepiad pollination. *Plant Syst. Evol.* 176, 227–253.

Lack A. J. (1977) Genets feeding on nectar from *Maranthes*

https://doi.org/10.1079/IJT20045 Published online by Cambridge University Press

polyandra in northern Ghana. *E. Afr. Wildlife J.* 15, 233–234.

Lack A. J. (1978) The ecology of the flowers of the savanna tree *Maranthes polyandra* and their visitors, with particular reference to bats. *J. Ecol.* 66, 287–295.

Ladd P. G. (1994) Pollen presenters in flowering plants – form and function. *Bot. J. Linn. Soc.* 115, 165–195.

Ladd P. G. and Donaldson J. S. (1993) Pollen presenters in the South African flora. *S. Afr. J. Bot.* 59, 465–477.

Latham P. (2001) Oyster nut *Telfairia pedata* (Sims) Hook. *Cucurbit Network News* 8(2), 1–2.

Liede S. and Whitehead V. (1991) Studies in the pollination biology of *Sarcostemma viminale* R. Br. sensu latu. *S. Afr. J. Bot.* 57, 115–122.

Linder H. P. and Midgley J. (1996) Anemophilous plants select their own pollen from the air. *Oecologia* 108, 85–87.

Le Maitre D. C. and Midgley J. J. (1992) Plant reproductive ecology, pp. 135–174. In *The Ecology of Fynbos* (Edited by R. M. Cowling). Oxford University Press, Cape Town.

Le Roux L. G. and Robbertse P. J. (1997) Aspects relating to seed production in *Gloriosa superba* L. *S. Afr. J. Bot.* 63, 191–197.

Le Roux L. G., Robbertse P. J. and van der Merwe C. F. (1996) The transmitting tract in *Gloriosa superba*: structure, pistil exudate and pollen tube growth. *S. Afr. J. Bot.* 62, 204–208.

Leston D. and Gibbs D. G. (1969) Phenology of cocoa and some associated insects in Ghana, pp. 197–204. *III. International Cocoa Research Conference Accra, Ghana, 23–29 November, 1969.*

Leston D. (1970) Entomology of the cocoa farm. *Annu. Rev. Ent.* 15, 273–294.

Lock J. M. (1980) Notes on *Aframomum* (Zingiberaceae) in West Africa, with a new key to the species. *Kew Bull.* 35, 299–313.

Lock J. M. and Hall J. B. (1981) Floral biology of *Mallotus oppositifolius* (Euphorbiaceae). *Biotropica* 14, 153–155.

Lock J. M. and Profita J. (1975) Pollination of *Eulophia cristata* (Sw.) Steud. (Orchidaceae) in southern Ghana. *Acta Bot. Neel.* 24, 135–138.

Lowrey T. K. and Robinson E. R. (1988) The interaction of gynomonoecy, dichogamy, and wind pollination in *Gunnera perpensa* L. (Gunneraceae) in South Africa. *Monographs in systematic botany, Missouri Botanical Garden* 25, 237–246.

Lorougnon G. (1973) Le vecteur pollinique chez les *Mapania* et les Cyperacees de sous-bois des forets tropicales ombrophiles. *Bull. Jard. Bot. National Belg.* 43, 33–36.

Meve U. and Liede S. (1994) Floral biology and pollination in stapeliads–new results and a literature review. *Plant Syst. Evol.* 192, 99–116.

Midgley J. (1989) Pollen dispersal distances for a conifer canopy species in the Knysna Forest. *S. Afr. J. Bot.* 55, 662–663.

Mostert D. P., Siegfried W. R. and Louw G. N. (1980) *Protea* nectar and satellite fauna in relation to the food requirements and pollinating role of the Cape sugarbird. *S. Afr. J. Sci.* 409–412.

MacGilillivray D. B. (1987) A centrifuging method for the removal of insect pollen loads. *J. Ent. Soc. Sth. Afr.* 50, 522–523.

Manning J. C. and Brothers D. J. (1986) Floral relations of four species of *Rediviva* in Natal (Hymenoptera: Apoideae: Mellitidae). *J. Ent. Soc. Sth. Afr.* 49, 107–114.

Manning J. C. and Goldblatt P. (1995) Cupid comes in many guises: the not-so-humble fly and a pollination guild in the Overberg. *Veld and Flora* 81(2), 50–52.

Manning J. C. and Goldblatt P. (1996) The *Prosoeca peringueyi* (Diptera: Nemestrinidae) pollination guild in southern Africa: long tongued flies and their tubular flowers. *Ann. Mo. Bot. Gard.* 83, 67–86.

Manning J. C. and Goldblatt P. (1997) The *Moegistorhynchus longirostris* (Diptera: Nemestrinidae) pollination guild: long-tubed flowers and a specialised long-proboscid fly pollination system in southern Africa. *Plant Syst. Evol.* 206, 51–69.

Manning J. C., Goldblatt P. and Winter P. J. D. (1999) Two new species of *Gladiolus* (Iridaceae: Ixioideae) from South Africa and notes on long-proboscid fly pollination in the genus. *Bothalia* 29, 217–223.

Manning J. C. and Linder H. P. (1992) Pollinators and evolution in *Disperis* (Orchidaceae) or why are there so many species? *S. Afr. J. Sci.* 88, 38–49.

Marais E. M. (1999) Ideas on the pollination of *Pelargonium* sect. Hoarea (Geraniaceae), pp. 105–115. In *African Plants: Biodiversity, Taxonomy and Uses* (Edited by J. Timberlake and S. Kativu) Royal Botanic Gardens, Kew.

Marloth R. (1908) Some observations on entomophilous flowers. *S. Afr. J. Sci.* 5, 110–113.

Marshall A. G. (1983) Bats, flowers and fruit: evolutionary relationships in the Old World. *Biol. J. Linn. Soc.* 20, 115–135.

McCall C. and Primack R. B. (1992) Influence of flower characteristics, weather, time of day and season on insect visitation rates in three plant communities. *Am. J. Bot.* 79, 434–442.

McDonald J. H. (1930) *Coffee Growing: With Special Reference to East Africa*. East Africa Ltd, London.

McDonald D. J. and van der Walt J. J. A. (1992) Observations on the pollination of *Pelargonium tricolor*, Section Campylia (Geraniaceae). *S. Afr. J. Bot.* 58, 386–392.

Milton S. J. and Moll E. J. (1982) Phenology of Australian Acacias in the S.W. Cape, South Africa, and its implications for management. *Bot. J. Linn. Soc.* 84, 295–327.

Moustafa M. A. and El Berry A. A. (1974) A study on the wild bees, *Osmia latreillei* SPIN and *O. submicans* MOR as pollinators to some economic crops in Egypt. *Ann. Agric. Sci.* 3, 233–240.

Murray M. G. (1985) Figs (*Ficus* spp.) and fig wasps (Chalcidoidea, Agaonidae): hypotheses for an ancient symbiosis. *Biol. J. Linn. Soc.* 26, 69–81.

Naicker S. and Baijnath H. (1982) Some interesting observations on pollination of *Ficus ingens*. *S. Afr. J. Bot.* 1, 82.

Newton L. E., Newton F. L. S. and Lomo A. (1979) The pollination of *Ficus vogelii* in Ghana. *Bot. J. Linn. Soc.* 78, 21–30.

Nicolson S. W. and Worswick P. V. (1990) Sodium and potassium concentrations in floral nectars in relation to foraging by honey bees. *S. Afr. J. Zool.* 25, 93–96.

Nilsson L. A. and Rabakonandranina E. (1988) Hawk-moth scale analysis and pollination specialization in the epilithic Malagasy endemic *Aerngis ellisii* (Reichenb. fil.) Schltr. (Orchidaceae). *Bot. J. Linn. Soc.* 97, 49–61.

Nilsson L. A., Jonsson L., Rason L. and Randrianjohany E. (1985a) Monophily and pollination mechanisms in *Angraecum arachnites* Schltr. (Orchidaceae) in a guild of long-tongued hawkmoths (Sphingidae) in Madagascar. *Biol. J. Linn. Soc.* 1.

Nilsson L. A., Jonsson L., Rason L. and Randrianjohany E. (1985b) Pollination of *Plectranthus vestitus* (Lamiaceae) by trap-lining hovering bees in Madagascar. *Plant. Syst. Evol.* 150, 223–236.

Nilsson L. A., Jonsson L., Rason L. and Randrianjohany E. (1986) The pollination of *Cymbidiella flabellata* (Orchidaceae) in Madagascar: a system operated by sphecid wasps. *Nord. J. Bot.* 6, 411–422.

Nilsson L. A., Jonsson L., Ralison L. and Randrianjohany E. (1987) Angraecoid orchids and hawkmoths in Central Madagascar: specialized pollination systems and generalized foragers. *Biotropica* 19, 310–318.

Nilsson L. A. (1992) Long pollinia on eyes: Hawk-moth pollination of *Cynorkis uniflora* Lindley (Orchidaceae) in Madagascar. *Biol. J. Linn. Soc.* 109, 145–160.

Nilsson L. A., Rabakonandrianina E., Pettersson B. and Grunmeir R. (1993) Lemur pollination in the Malagasy rainforest liana *Strongylodon craveniae* (Leguminosae). *Evolutionary Trends in Plants* 7, 49–56.

Norstog K. (1987) Cycads and the origin of insect pollination. *Am. Sci.* 75, 270–279.

Nur N. (1976) Studies on pollination in Musaceae. *Ann. Bot.* 40, 167–177.

Onim J. F. M., Pathak R. S. and van Eijnatten C. L. M. (1979) Influence of insect pollinators on the degree of outcrossing in pigeon pea in Kenya, pp. 211–218. In *Proceedings IVth International Symposium on Pollination, Maryland Agricultural Experiment Station. Special Miscellaneous Publication.*

Onim J. F. M., van Eijnatten C. L. M. and Pathak R. S. (1979b) Some factors which encourage outcrossing in pigeon pea, pp. 219–225. In *Proceedings IVth International Symposium on Pollination, Maryland Agricultural Experiment Station. Special Miscellaneous Publication.*

Ornduff R. and Dulberger R. (1978) Floral enantiomorphy and the reproductive system of *Wachendorfia paniculata* (Haemodoraceae). *New Phytol.* 80, 427–434.

Ortega-Olivencia A. and Devesa J. A. (1988) Taxonomy and breeding system in a new species of *Scrophularia* L. (Scrophulariaceae) from Morocco. *Bot. J. Linn. Soc.* 128, 185–202.

Osborne R., Robbertse P. J. and Claassen M. I. (1992) The longevity of cycad pollen in storage. *S. Afr. J. Bot* 58, 250–254.

Osmaston H. A. (1965) Pollen and seed dispersal in *Chlorophora excelsa* and other Moraceae, and in *Parkia filicoidea* (Mimosaceae), with special reference to the role of the fruit bat, *Eidolon helvum*. *Commonw. Forest. Rev.* 44, 96–104.

Owens S. J. (1981) Self-incompatibility in the Commelinaceae. *Ann. Bot.* 47, 567–81.

Pettet A. (1977) Seasonal changes in nectar-feeding by birds at Zaria, Nigeria. *Ibis* 119, 291–308.

Phillips S. M. (1999) A review of African forest grasses, pp. 3–9. In *African Plants: Biodiversity, Taxonomy and Uses* (Edited by J. Timberlake and S. Kativu). Royal Botanic Gardens, Kew.

Picker M. D. and Midgley J. J. (1996) Pollination by monkey beetles (Coleoptera: Scarabaeidae: Hopliini): flower and colour preferences. *Afr. Entomol.* 4, 7–14.

Pieterse P. and Cairns A. L. P. (1988) Factors affecting the reproductive success of *Acacia longifolia* (Andr) Willd in the Banhoek Valley, south-western Cape, Republic of South Africa. *S. Afr. J. Bot.* 54, 461–464.

Posnette A. F. (1938) Incompatibility and pollination in cacao. *Rep. Cacao Res.* 7, 19–20.

Posnette A. F. (1942a) Natural pollination of cocoa *Theobroma leiocarpa*, on the Gold Coast: I. *Trop. Agric. Trin.* 19, 12–16.

Posnette A. F. (1942b) Natural pollination of cocoa *Theobroma leiocarpa* Bern. On the Gold Coast: II. *Trop. Agri. Trin.* 19, 188–191.

Posnette A. F. (1950) The pollination of cacao in the Gold coast, *J. Hort. Sci.* 25, 155–163.

Potgieter C. J., Edwards T. J., Miller R. M. and van Staden J. (1999) Pollination of seven *Plectranthus* spp. (Lamicaeae) in southern Natal, South Africa. *Plant Syst. Evol.* 218, 99–112.

Prendergast H. D. V. (1982) Pollination of *Hibiscus rosa-sinensis*. *Biotropica* 14, 288.

Ramirez B. W. (1969) Fig wasps: mechanism of pollen transfer. *Science* 163, 580–581.

Ramirez W. (1970) Host specificity of fig wasps (Agaonidae). *Evolution* 24, 680–691.

Rashad S. E. (1978) *Utilisation of non-Apis bees as crop pollinators (EG-ARS-66): first annual report (1978)*. Cairo University, Giza, Egypt. 48 pp.

Rashad S. E. and Moustafa M. A. (1973) Distribution and life history of *Andrena ovaltula* (K.) in Egypt. *Mitt. Zool. Mus. Berl* 49, 327–331.

Rashad S. E., Ewies M. A. and El-Rabie H. G. (1978) Pollinators of peanut (*Arachis hypogaea* L.) and the effect of honeybees on its yield, pp. 235–239. In *Proceedings IVth International Symposium on Pollination, Maryland Agricultural Experiment Station. Special Miscellaneous Publication.*

Rashad S. E., Ewies M. A. and El-Rabie H. G. (1979) Insect pollinators of sesame (*Sesame indicum* L.) with special reference to the role of honeybees, pp. 231–234. In *Proceedings IVth International Symposium on Pollination.*

Maryland Agricultural Experimental Station Miscellaneous Publication.

Rasplus J. Y. (1996) The one-to-one species specificity of the *Ficus*–Agaoninae mutualism: how casual?, pp. 639–649. In *The Biodiversity of Afr. Plants* (Edited by L. J. G. van der Maesen, X. M. Van der Burgt and J. M. van Medenbach de Rooy). Kluwer Academic Publishers, Dordrecht.

Ratsirarson J. (1995) Pollination ecology of *Aloe divaricata* Berger (Liliaceae): an endemic plant species of southwest Madagascar. *S. Afr. J. Bot.* 61 249–252.

Raven P. H. (1977) *Erythrina* symposium II; *Erythrina* (Fabaceae): introduction to symposium II. *Lloydia* 40, 401–406.

Rawal K. M., Bryant P., Rachie K. O. and Porter W. M. (1978) Cross-pollination studes of male-sterile genotypes in cowpeas. *Crop. Sci.* 18, 283–285.

Rebelo A. G. (1985) Might mites pollinate Proteas? *S. Afr. J. Sci.* 81, 694.

Rebelo A. G. (Ed.) (1987a) *A Preliminary Synthesis of Pollination Biology of the Cape Flora*. Council for Scientific and Industrial Research, Pretoria. 257 pp.

Rebelo A. G. (1987b) Bird pollination in the Cape flora, pp. 83–108. In *A Preliminary Synthesis of Pollination Biology of the Cape Flora* (Edited by A. G. Rebelo). Council for Scientific and Industrial Research, Pretoria.

Rebelo A. G. (1987c) Management implications, pp. 193–211. In *A Preliminary Synthesis of Pollination Biology of the Cape Flora* (Edited by A. G. Rebelo). Council for Scientific and Industrial Research, Pretoria.

Rebelo A. G. (1987d) Visits to *Oldenburgia grandis* (Thunb.) Baillon (Asteraceae) by the Cape sugarbird *Proerops cafer*. *Ostrich* 58, 186–187.

Rebelo A. G. (1987e) Sunbird feeding at *Satyrium odorum* Sond. flowers. *Ostrich* 50, 185–186.

Rebelo A. G. and Breytenbach C. J. (1987) Mammal pollination in the Cape flora pp 109–125. In *A Preliminary Synthesis of Pollination Biology of the Cape Flora* (Edited by A. G. Rebelo). Council for Scientific and Industrial Research, Pretoria.

Rebelo A. G. and Jarman M. L. (1987) Pollination and community ecology, pp. 155–192. In *A Preliminary Synthesis of Pollination Biology of the Cape Flora* (Edited by A. G. Rebelo). Council for Scientific and Industrial Research, Pretoria.

Rebelo A. G. and Siegfried W. R. (1985) Colour and size of flowers in relation to pollination of *Erica* species. *Oecologia* 65, 584–590.

Reese G. (1973) The structure of the highly specialized carrion-flowers of the stapeliads. *Cactus and Succulent Journal of the Cactus and Succulent Society of America* 45, 18–29.

Rourke J. P. (1972) Taxonomic studies on *Leucospermum* R. *Br. J. S. Afr. Bot. Supplementary Volume* 8, 177–179.

Rourke J. P. (1988) A new species of *Mimetes* (Proteaceae) from the southern Cape. *S. Afr. J. Bot.* 54, 636–639.

Rourke J. P. and Wiens D. (1977) Convergence floral evolution in South African and Australian Protaceae and its possible bearing on pollination by nonflying mammals. *Ann. Bot. Mo. Gard.* 64, 1–17.

Rowan M. K. (1974) Bird pollination of *Strelitzia*. *Ostrich* 45, 40.

Rowley F. D. (1980) The pollination mechanism of *Adenium* (Apocynaceae). *National Cactus and Succulent Journal, UK* 35, 2–5.

Sampson H. C. (1936) Cultivated crop plants of the British Empire and Anglo-Egyptian Sudan (Tropical and Subtropical) *Addit. Ser. Kew* 12.

Scholtz A. (1987) Pollination biology and the fossil record, pp. 6–21. In *A Preliminary Synthesis of Pollination Biology of the Cape Flora* (Edited by A. G. Rebelo). Council for Scientific and Industrial Research, Pretoria.

Scott, G. (1991) A revision of *Cyanella* (Tecophilaeaceae) excluding *C. amboensis*. *S. Afr. J. Bot.* 57, 34–54.

Scott Elliot G. F. (1890a) Note on the fertilization of *Musa, Strelitzia reginae* and *Ravenala madagascarensis*. *Ann. Bot.* 4, 259–263.

Scott Elliot G. F. (1890b) Ornithophilous flowers in South Africa. *Ann. Bot.* 4, 265–280.

Shawer M. B., Salem M. M. and Saleh R. S. (1989) Survey of insect pollinators of Egyptian clover, *Trifolium alexandrinum* L. at Kafr El-Sheikh, Egypt, pp. 134–137. In *Proceedings 4th International Conference on Agriculture in Tropical Climates, Cairo, 1988*.

Singh Y., Van Wyk A. E. and Baijnath H. (1996) Floral biology of *Zantedeschia aethiopica* (L.) Spreng. (Araceae). *S. Afr. J. Bot*. 62, 146–150.

Skead C. J. (1975) Weaverbird pollination of *Strelitzia reginae*. *Ostrich* 46, 183–185.

Smith F. G. (1958) Beekeeping operations in Tanganyika, 1949–1957. *Bee Wld* 39, 29–36.

Smith G. F., Theron P. D. and Loots G. C. (1992) Notes on the microfaunal complement of *Poellnitzia rubriflora* (Asphodelaceae: Aloideae): an example of a mite-flower domatia association. *Taxon* 41, 437–450.

Soderstrom R. T. and Calderon C. E. (1971) Insect pollination in tropical rain forest grasses. *Biotropica* 3, 1–16.

Soria J. (1971) A preliminary report on experiments of hand pollination and fertilizers in cacao, pp. 608–613. In *Third International Cocoa Research Conference, 1969*. Cocoa Research Institute, Tafo, Ghana.

Soria S. de J. and Bystrak P. G. (1975) A new species of *Forcipomyia* (Diptera, Ceratopoognidae) described in all stages, with an account of its role as a cacao pollinator. *Revista Theobroma* 5, 3–11.

Soria S. de J. (1970) Studies on *Forcipomyia* spp. midges (Diptera, Ceratopogonidae) related to the pollination of *Theobroma cacao* L. PhD thesis, University of Wisconsin, Wisconsin.

Steiner K. E. (1987) Breeding systems in the Cape flora, pp. 22–51. In *A Preliminary Synthesis of Pollination Biology of the Cape Flora* (Edited by A. G. Rebelo). Council for Scientific and Industrial Research, Pretoria.

Steiner K. E. (1988) Dioecism and its correlates in the Cape flora of South Africa. *Am. J. Bot.* 75, 1742–1754.

Steiner K. E. (1989a) A new species of *Diascia* (Scrophulariaceae) from the southern Drakensberg. *S. Afr. J. Bot.* 55, 250–253.
Steiner K. E. (1989b) The pollination of *Disperis* (Orchidaceae) by oil-collecting bees in southern Africa. *Lindleyana* 4, 164–183.
Steiner K. E. (1990) The *Diascia* (Scrophulariaceae) window: an orientation cue for oil-collecting bees. *Bot. J. Linn. Soc.* 102, 175–195.
Steiner K. E. (1992) Two new *Diascia* species (Scrophulariaceae) from the Little Karoo. *S. Afr. J. Bot.* 58, 39–47.
Steiner K. E. (1993) Has *Ixianthes* (Scrophulariaceae) lost its special bee? *Plant Syst. Evol.* 185, 7–16.
Steiner K. E. (1995) Three new *Diascia* species from arid areas of the Western and Northern Cape provinces, South Africa. *S. Afr. J. Bot.* 61, 72–79.
Steiner K. E. (1998a) Beetle pollination of peacock moraes (Iridaceae) in South Africa. *Plant Syst. Evol.* 209, 47–65.
Steiner K. E. (1998b) The evolution of beetle pollination in a South African orchid. *Am. J. Bot.* 85, 1180–1193.
Steiner K. E. (1999) A new species of *Diascia* (Scrophulariaceae) from the Eastern Cape (South Africa) with notes on other members of the genus in that region. *S. Afr. J. Bot.* 65, 223–231.
Steiner K. E. and Whitehead V. B. (1988) The association between oil-producing flowers and oil-collecting bees in the Drakensberg of Southern Africa. *Modern Systematic Studies in African Botany, Monographs in Systematic Botany of the Missouri Botanical Garden* 19.
Steiner K. E. and Whitehead V. B. (1990) Pollinator adaptation to oil-secreting flowers–*Rediviva* and *Diascia*. *Evolution* 44, 1701–1707.
Steiner K. E. and Whitehead V. B. (1991a) Oil flowers and oil bees: further evidence for pollinator adaptation. *Evolution* 45, 1493–1501.
Steiner K. E. and Whitehead V. B. (1991b) Resin collection and the pollination of *Dalechampia capensis* (Euphorbiaceae) by *Pachyanthidium cordatum* (Hymenoptera: Megachilidae) in South Africa. *J. Ent. Soc. S. Afr.* 67–72.
Steiner K. E. and Whitehead V. B. (1996) The consequences of specialisation for pollination in a rare South African shrub, *Ixianthes retzioides* (Scropulariaceae). *Plant Syst. Evol.* 201, 131–138.
Steiner K. E. Whitehead V. B. and Johnson S. D. (1994) Floral and pollinator divergence in two sexually deceptive South African orchids. *Am. J. Bot.* 81, 185–194.
Steyn E. M. A. and Robbertse P. J. (1988) Flower production and sexuality in *Bequartiodendron magalismontanum*. *S. Afr. J. Bot.* 54, 481–486.
Steyn E. M. A. and Robbertse P. J. (1990) Fruit production in a morphologically gynodioecious population of *Bequaertiodendron magalismontanum*. *S. Afr. J. Bot.* 56, 6–10.
Stirton C. H. (1976) *Thuranthos*: notes on generic status, morphology and pollination biology. *Bothalia* 12, 161–165.
Stirton C. H. (1977a) A note on the flowers of *Halleria lucida*. *Bothalia* 12, 223–224.
Stirton C. H. (1977b) The pollination of *Canabalia virosa* by xylocopid and megachilid bees. *Bothalia* 12, 225–227.
Stirton C. H. (1977c) Broad spectrum pollination of *Plectranthus neochilus*. *Bothalia* 12, 229–230.
Stone G. N., Gilbert F., Willmer P. G., Potts S., Semida F. and Zalat S. (1999) Windows of opportunity and the temporal structuring of foraging activity in a desert solitary bee. *Ecol. Entomol.* 24, 208–221.
Stone G. N., Willmer P. G. and Nee S. (1996) Daily partitioning of pollinators in an *Acacia* community. *Proc. Ro. Soc. B* 263: 1389–1393.
Stone G. N., Willmer P. G. and Rowe J. A. (1998) Partitioning of pollinators during flowering in an African *Acacia* community. *Ecology* 79, 2808–2827.
Struck M. (1997) Floral divergence and convergence in the genus *Pelargonium* (Geraniaceae) in southern Africa: ecological and evolutionary considerations. *Plant Syst. Evol.* 208, 71–97.
Struck M. and van der Walt J. J. A. (1996) Floral structure and pollination in *Pelargonium*, pp. 631–638. In *The Biodiversity of African Plants* (Edited by L. J. G. van der Maesen, X. M. Van der Burgt and J. M. van Medenbach de Rooy). Kluwer Academic Publishers, Dordrecht.
Sussman R. W. and Raven P. H. (1978) Pollination by lemurs and marsupials: an archaic co-evolutionary system. *Science* 200, 731–736.
Sussman M. and Tattersall I. (1976) Cycles of activity, group composition, and diet of *Lemur mongoz mongoz* Linnaeus 1766 in Madagascar. *Folia Primatol.* 26, 270–283.
Syed R. A. (1979) Studies on oil palm pollination by insects. *Bull. Entomol. Res.* 69, 213–224.
Tay K. C. (1981) Observations on insects visiting oil palm infloresences. *Planter* 57, 62–81.
Tobgy H. A. and Said I. (1956) Some factors influencing seed setting in berseem or Egyptian clover (*Trifolium alexandrinum* L. *First Meeting Working Party on Grazing and Fodder Research Near East, Cairo University.*
Trought T. (1930) Notes on certain facts on vicinism and artificial pollination in Egypt. *Emp. Cott. Grow. Rev.* 7, 13–18.
Ueckermann C. and van Rooyen M. W. (2000) Insect pollination and seed set in four ephemeral plant species from Namaqualand. *S. Afr. J. Bot.* 66, 28–30.
van der Merwe A. M. and Marais E. M. (2001) A new species of *Polyxena* (Hyacinthaceae, tribe Massoniae) from Komsberg, Northern Cape Province. *S. Afr. J. Bot.* 67, 44–46.
van der Pijl L. (1954) *Xylocopa* and flowers in the tropics. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, Ser.* C57, 413–423, 541–562.
van der Walt I. D. and Littlejohn G. M. (1996) Stigma receptivity of two *Protea* cultivars in relation to the development of hybridization techniques. *S. Afr. J. Bot.* 62, 258–262.
van der Walt J. J. A., McDonald D. J. and van Wyk N. (1990) A new species of *Pelargonium* with notes on its ecology and pollination biology. *S. Afr. J. Bot.* 56, 467–470.

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van Noordt S., Ware A. B. and Compton S. G. (1989) Pollinator specific volatile attractants released from the figs of *Ficus burtt-davyi*. *S. Afr. J. Sci.* 85, 323–324.

van Rensburg J. G. L. and Robbertse P. J. (1988) Seed development of *Ornithogalum dubium*, with special reference to fertilization and the egg apparatus. *S. Afr. J. Bot.* 54, 196–202.

van Wyk A. E. and Lowrey T. K. (1988) Studies on the reproductive biology of *Eugenia* L. (Myrtaceae) in southern Africa. *Monographs in systematic botany, Missouri Botanical Garden* 25, 279–293.

Venter H. M. (1996) Difficulties with cross-pollinating five cow-pea lines: technique and development. In *The Biodiversity of African Plants* (Edited by L. J. G. van der Maesen, X. M. Van der Burgt and J. M. van Medenbach de Rooy). Kluwer Academic Publishers.

Voelcker O. J. (1937) Self-incompatibility in cacao. *Rep. Cacao Res.* 6, 2.

Voelcker O. J. (1938) Self-incompatibility in cacao II. *Rep. Cacao Res.* 7, 2.

Voelcker O. J. (1940) The degree of cross-pollination in cacao in Nigeria. *Trop. Agric. Trin* 17, 184–186.

Vogel S. (1954) *Blütenbiologische Typen als Elemente der Sippengliederung, dargestellt anhand der Flora Südafrikas. Bot. Studien I.* Fischer, Jena, 358 pp.

Vogel S. (1984) The *Diascia* flower and its bee – an oil-based symbiosis in southern Africa. *Acta Bot. Neerl.* 33, 509–518.

Wafa A. K. and Hanna S. (1959) Effect of the honeybee as a pollinating agent on the yield of beans and clover in Cairo, Egypt. *Elfelaha J.* 4, 1–28; 5, 1–19.

Wafa A. K. and Ibrahim S. H. (1957a) The honeybee as an important insect for pollination. *Bull, Fac. Agric. Ain Shams Univ.* 162.

Wafa A. K. and Ibrahim S. H. (1957b) The honeybee as an important insect for pollination *Bull. Fac. Agric. Ain Shams Univ.* 164.

Wafa A. K. and Ibrahim S. H. (1959) Pollinators of the chief sources of nectar and pollen grain plants in Egypt. *Bull. Soc. Ent. Egypte* 43, 133–154.

Wafa A. K. and Ibrahim S. H. (1960a) The effect of the honeybee as a pollinating agent on the yield of clover and cotton. *Bull. Fac. Agric. Ain Shams Univ.* 206, 1–44.

Wafa A. K. and Ibrahim S. H. (1960b) Effect of the honeybee as a pollinating agent on the yield of orange. *Elfelaha J.* (Jan/Feb).

Wafa A. K. and Mohamed M. I. (1970) Anthophorinae pollinating on broad bean flowers. *Bull. Soc. Ent. Egypte* 54, 213–220.

Wafa A. K., Ibrahim S. H. and Eweis M. A. (1972) Studies on the effect of the honey bee as a pollinator on the yield of alfalfa, *Medicago sativa* L. (Hymenoptera: Apidae). *Bull. Soc. Ent. Egypte* 56, 273–285.

Wafa A. K., Ibrahim S. H. and Eweis M. A. (1975) Insect pollinators of alfalfa, *Medicago sativa* L. *Agric. Res. Rev.* 53, 199–207.

Wafa A. K., Rashad S. E. and Eweis M. A. (1974) The efficiency of honeybees in pollinating alfalfa in Giza region (Hymenoptera: Apidae). *Bull. Soc. Ent. Egypte* 58, 117–121.

Ware A. B. and Compton S. G. (1992) Breakdown of pollinator specificity in an African fig tree. *Biotropica* 24, 544–549.

Watmough R. H. (1974) Biology and behaviour of carpenter bees in southern Africa. *J. Ent. Soc. Sth. Afr.* 37, 261–281.

Webster C. C. (1943) A note on pollination in budded plantation of Tung Trees (*Aleurites montena*). *Nyasaland Agric. Quart. J.* 3, 17–19.

Westerkamp C. (1990) Bird flowers: hovering versus perching exploitation. *Bot. Acta* 103, 366–371.

Wharton R. A., Tilson J. W. and Tilson, R. L. (1980) Asynchrony in a wild population of *Ficus sycomorus* L. *S. Afr. J. Sci.* 76, 478–480.

Whitehead V. B., Schelpe E. A. C. L. E. and Anthony N. C. (1984) The bee, *Rediviva longimanus* Michener (Apoideae: Melittidae), collecting pollen and oil from *Diascia longicornis* (Thunb.) Druce (Scrophulariaceae). *S. Afr. J. Sci.* 80, 286.

Whitehead V. B., Giliomee J. H. and Rebelo A. G. (1987) Insect pollination in the Cape flora, pp. 52–82. In *A Preliminary Synthesis of Pollination Biology in the Cape Flora* (Edited by A. G. Rebelo). Council for Scientific and Industrial Research, Pretoria.

Wiebes J. T. (1979) Co-evolution of figs and their insect pollinators. *Annu. Rev. Ecol. Syst.* 10, 1–12.

Wiens D. and Rourke J. P. (1978) Rodent pollination in Southern African *Protea* spp. *Nature* 276, 71–73.

Wiens D., Rourke J. P., Casper B. B., Rickert E. A., Lapine T. R., Peterson C. J. and Channing A. (1983) Nonflying mammal pollination of Southern African *Proteas*: a non-coevolved system. *Ann. Mo. Bot. Gard.* 70, 1–31.

Williams I. J. M. (1972) A revision of the genus *Leucodendron* (Proteaceae). *Contr. Bolus Herb.* 3, 401–402.

Willmer P. G. and Stone G. N. (1997) Ant deterrence in *Acacia* flowers: how aggressive ant-guards assist seed-set. *Nature* 388, 165–167.

Wright M. G. (1994) Seed production by *Protea laurifolia* (Proteaceae) after insect versus insect and bird pollination: a quality difference? *S. Afr. J. Sci.* 90, 199.

Wright M. G., Visser D. and de Lange J. H. (1991) Autecological studies on *Audouinia capitata* (Bruniaceae). 2. Insects as pollen vectors. *S. Afr. J. Bot.* 57, 260–263.

Wright M. G., Wright G. E. P. and Smith, P. (1989) Entemophily and seed predation of *Witsenia maura* (Iridaceae) a rare fynbos species. *S. Afr. J. Bot.* 55, 273–277.

Wright M. G., Visser D., Coetzee J. H. and Giliomee J. H. (1991) Insect and bird pollination of *Protea* species in the western Cape: further data. *S. Afr. J. Sci.* 87, 214–215.