Pollination syndromes of *Erica* species in the south-western Cape

A.G. Rebelo, W.R. Siegfried and E.G.H. Oliver
FitzPatrick Institute, University of Cape Town and Botanical Research Unit, Stellenbosch

The 426 species of the genus *Erica* L. in the south-western Cape are categorized according to their principal putative pollinating agents, based on the shape of the flowers and field observations. Wind pollination is restricted to 21 species in the genus *Erica*; most of the more specialized wind-pollinated species in the subfamily Ericoideae being assigned to the closely related genus *Philippia* Klotzsch and other genera of the tribe Salaxideae. Sixty-six *Erica* species are bird-pollinated and display two main flower shapes: tubular and tubular-curved; the former being divided into brush and tube flowers based on anther morphology. The majority (80%) of *Erica* species are insect-pollinated, and several subcategories can be assigned. The most distinctive subcategory is that of rhinomyiophily (pollination by dipterans with long proboscises) which accounts for 9% of all insect-pollinated *Erica* species. The richness of insect-pollinated *Erica* species parallels a richness of insect species, among which anthophilous dipterans and hymenopterans feature prominently.
S. Afr. J. Bot. 1985, 51: 270 – 280

Die 426 spesies van die genus *Erica* L. wat in die suidwes-Kaap voorkom, word geklassifiseer volgens hulle belangrikste moontlike bestuiwingsagente, gebaseer op blomvorms en waarnemings in die veld. Windbestuiwing is beperk tot slegs 21 *Erica* spesies; die meeste meer gespesialiseerde windbestuifde spesies in die subfamilie Ericoideae behoort aan die naverwante genus *Philippia* Klotzsch en ander genera van die Salaxideae stam. Ses-en-sestig *Erica* spesies word deur voëls bestuif en vertoon hoofsaaklik twee blomvorms: buisvormig en boog-buisvormig; die eerste tipe word verdeel in borsel- en buisblomme, volgens helmknopmorfologie. Die meerderheid *Erica* spesies (80%) word deur insekte bestuif, en 'n aantal subkategorieë kan onderskei word. Die opvallendste subkategorie is dié van rhinomyiofilie (bestuiwing deur Diptera met lang monddele) wat 9% van alle insekbestuifde *Erica* spesies uitmaak. Die relatief groot aantal insekbestuifde *Erica* spesies weerspieël 'n hoë insekspesiesrykheid, waaronder die groot aantal blombesoekende Diptera en Hymenoptera opvallend is.
S.-Afr. Tydskr. Plantk. 1985, 51: 270 – 280

Keywords: Anemophily, entomophily, *Erica*, ornithophily, pollination, rhinomyiophily, taxonomy

A.G. Rebelo* and W.R. Siegfried
FitzPatrick Institute, University of Cape Town,
Rondebosch, 7700 Republic of South Africa

E.G.H. Oliver
Botanical Research Unit, P.O. Box 471, Stellenbosch,
7600 Republic of South Africa

*To whom correspondence should be addressed

Accepted 15 April 1985

Introduction

The Cape Floral Kingdom is characterized by a plant species richness which is much greater than that of any other temperate flora (Bond & Goldblatt 1984). *Erica* L. is the largest constituent genus of this flora (Oliver, Linder & Rourke 1983), and includes some 426 species in the south-western Cape region of South Africa. Some 175 species occur at the geographical locus of maximum *Erica* diversity, in an area of less than 625 km^2, with related genera contributing 27 more species (Oliver *et al.* 1983).

Very little is known about pollination processes in the Cape Floral Kingdom, and nothing is known about how pollen flow is maintained between so many co-occurring plant species. This knowledge is necessary for effective conservation management of the Cape Floral Kingdom (Siegfried 1983). More particularly, relatively few studies of pollination of *Erica* species have been made in the south-western Cape (Robertson 1980; Anderson, Buys & Johannsmeier 1983; Rebelo, Siegfried & Crowe 1984; Herrmann 1985), since general pollination syndromes in the genus were described provisionally by Scott-Elliot (1890), Marloth (1932) and Vogel (1954). Here we delimit and catalogue the probable pollination syndromes in the genus *Erica*, in order to highlight subjects for future research.

Methods

Pollination syndromes of *Erica* species in the south-western Cape (Figure 1) were determined primarily by the shape of the flowers on herbarium specimens (Figures 2 & 3), our field observations of putative pollinators and from the literature (Scott-Elliott 1890; Marloth 1932; Vogel 1954; Baker & Oliver 1967; Robertson 1980; Collins 1983; Rebelo *et al.* 1984; Herrmann 1985).

Anemophily (wind pollination) was attributed to species having large cyathiform or peltate stigmatic surface areas (several times the style diameter) relative to the flower size, irrespective of the flower shape. These species release large quantities of pollen when agitated in the field. The stigmatic surface, which apparently ceases to be receptive before the pollen is released (pers. obs.), is usually situated just outside the mouth of the flower.

Ornithophily (bird pollination) was assigned to species having long tubular flowers (Figures 2 & 3) with orifices wide enough (> 2 mm Ø) to accommodate the beaks of sunbirds (Nectariniidae).

A conspicuous feature of entomophily (insect pollination) in *Erica* is the presence of elaborate appendages borne by the anthers. These appendages position the anthers in the centre

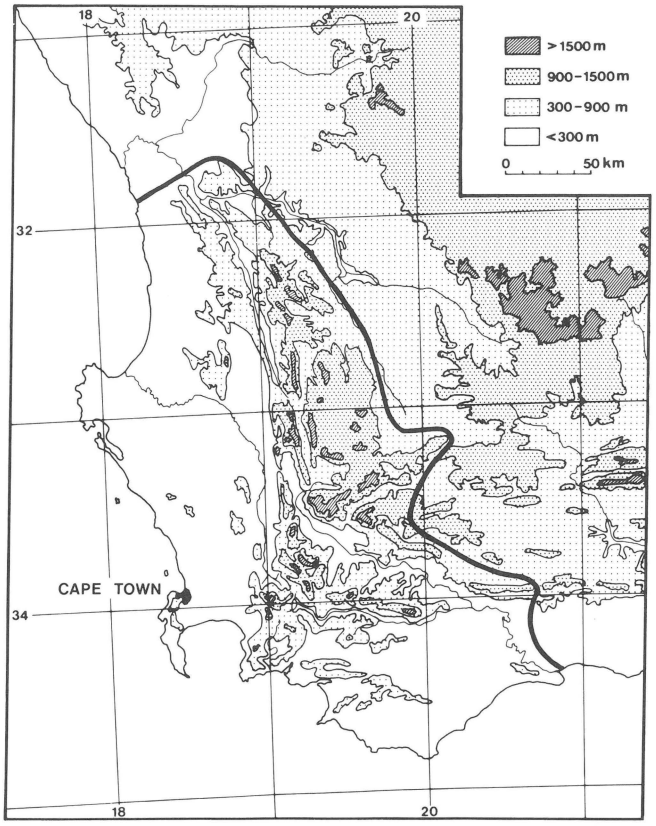

Figure 1 The area of the south-western Cape covered in this study.

of the corolla tube where they may optimally deposit pollen on visiting insects (Baker & Oliver 1967). Initially we attempted to subdivide insect-pollinated species according to moths, butterflies, flies and bees as the putative pollinating agents. However, many species have flowers with intermediate shapes, and the low rates of insect visitation observed in the field further restricted such a categorization. Because pollen morphology, from preliminary investigations, appears to be uniform within the genus, an examination of pollen carried by the various pollinating agents would not help in determining the number of different *Erica* species visited by pollinators (i.e. the degree of pollinator specificity). Moreover, because pollen morphology is uniform within the genus, it is of no value in delimiting pollination syndromes. A major problem in delimiting pollinator spectra in *Erica*, and of fynbos plant species in general, is the paucity of local entomological knowledge.

The most discrete insect-pollination syndrome in *Erica* is pollination by hovering dipterans having long proboscises. No specific term exists for this syndrome, which is quite different from both the fly and butterfly pollination syndromes which Vogel (1954) combined into his psychoidophilous syndrome. Here we use the term rhinomyiophily (the nose-fly syndrome) for pollination by hovering dipterans with long proboscises, although elsewhere (Rebelo & Siegfried 1985) we have allied it with the sphingophilous syndrome (pollination by hovering moths). [The 'i' is necessary in myiophily (*cf.* myophily — Faegri & Van der Pijl 1979) to indicate derivation from the Greek *Myia*, a fly, rather than *Mys*, a mouse (R.K. Brooke pers. comm.)].

Erica species pollinated by hovering dipterans with long proboscises are usually ampullaceous (flask-shaped) and have star-shaped corolla lobes. Potential pollen and nectar thieves are excluded by the very small mouths of the flowers. Although colour was not used in determining pollination syndromes, most LPF- (long proboscid fly) pollinated *Erica* species are light pink in colour, as in the classical hawkmoth-pollination syndrome, but are not known to produce noticeable nocturnal odours. Many have a small, red, coloured centre in the pale star-shaped corolla lobes, which surrounds the small corolla orifice. Only long-tubed ampullaceous species were assigned to the LPF-pollination syndrome, since short-tubed (< 10 mm) *Erica* species are visited by a variety of insects, including bees, butterflies and non-hovering dipterans (e.g. *E. caffra*).

Results and Discussion

Our extensive observations, made opportunistically in the field over several years, together with observations at the Kirstenbosch National Botanic Gardens, have resulted in a relatively clear delimitation of the bird-pollination syndrome. However, this and other syndromes delimited here are not exclusive, in that many apparently insect-pollinated, small, globular, open-mouthed *Erica* species which are visited extensively by insects during warm conditions, may, following protracted rains, be visited by sunbirds which feed frequently at the flowers for most of the day (pers. obs.).

The categorization of putatively insect-pollinated *Erica* species was complicated by an apparent lack of visits by insects (Robertson 1980; pers. obs.). This may be partly an artifact of our largely diurnal field observations, but brief nocturnal observations indicated that very few *Erica* species produce detectable nocturnal odours under conditions during which visits by moths to other fynbos plants (e.g. *Gnidia*) are readily apparent. Moreover, an assessment of the apparently low rate of visits by insects is complicated because many *Erica* species retain the shape and colour of their flowers until long after the ovaries begin developing.

The genus *Erica* is divided into 41 artificial (i.e. phenetic) sections, based largely on the shape of the corolla (Figure 2) and the size of the corolla relative to that of the calyx. Guthrie & Bolus (quoted by Baker & Oliver 1967) remark that the form of organs in this genus is unusually variable and results in closely allied species belonging to widely divergent taxonomic sections and even subgenera. This variation is so diverse that Palser & Murty (1967) suggest that extensive hybridization between widely divergent species must have occurred in order to account for the 'genus having as much variability as occurs in *Erica* and yet no distinct and recognizable groupings or lines of relationships'. However, these sections appear to be correlated with the principal pollination syndromes within the genus (Table 1; Appendix 1).

Many *Erica* flowers, regardless of putative pollination syndromes, have been observed during taxonomic investigations to be frequented by numerous microscopic thrips-like insects, which are reported to be of significance in *Erica* pollination in Europe (Hagerup 1950; Hagerup & Hagerup 1953). However, the majority of thrips-like insects observed on *Erica* species in the south-western Cape appear to be too small to be important pollinators (pers. obs.). Although the small size of these insects limits the number of pollen grains that each individual can carry to, on average, fewer than 4,0 (n = 430, data from Lewis 1973), they may account for most of the seed set in certain *Erica* species during protracted periods of inclement weather (Lewis loc. cit.). The possible role of these insects as pollinators urgently needs to be assessed in the south-western Cape.

We believe that autogamy is rare among *Erica* species in the south-western Cape, because collapse of the stigma pre-

cedes pollen release. This is most evident in the many small-flowered species and may signal reduced stigma receptivity. In Europe, *Erica cinerea* L. is visited by a large variety of insect species (Knuth 1906) which probably pollinate it. In the Faroes, however, where there is a paucity of insect pollinators (Hagerup 1951), *E. cinerea* may release its pollen by spontaneous rupture of the anther ring before anthesis, thereby effecting self-pollination (bud autogamy) (Hagerup 1950). [Pollinator exclusion experiments were, however, apparently not undertaken (Hagerup & Hagerup 1953).] Pre-anthesis rupture of the anther ring does not occur in the majority of *Erica* species in the south-western Cape.

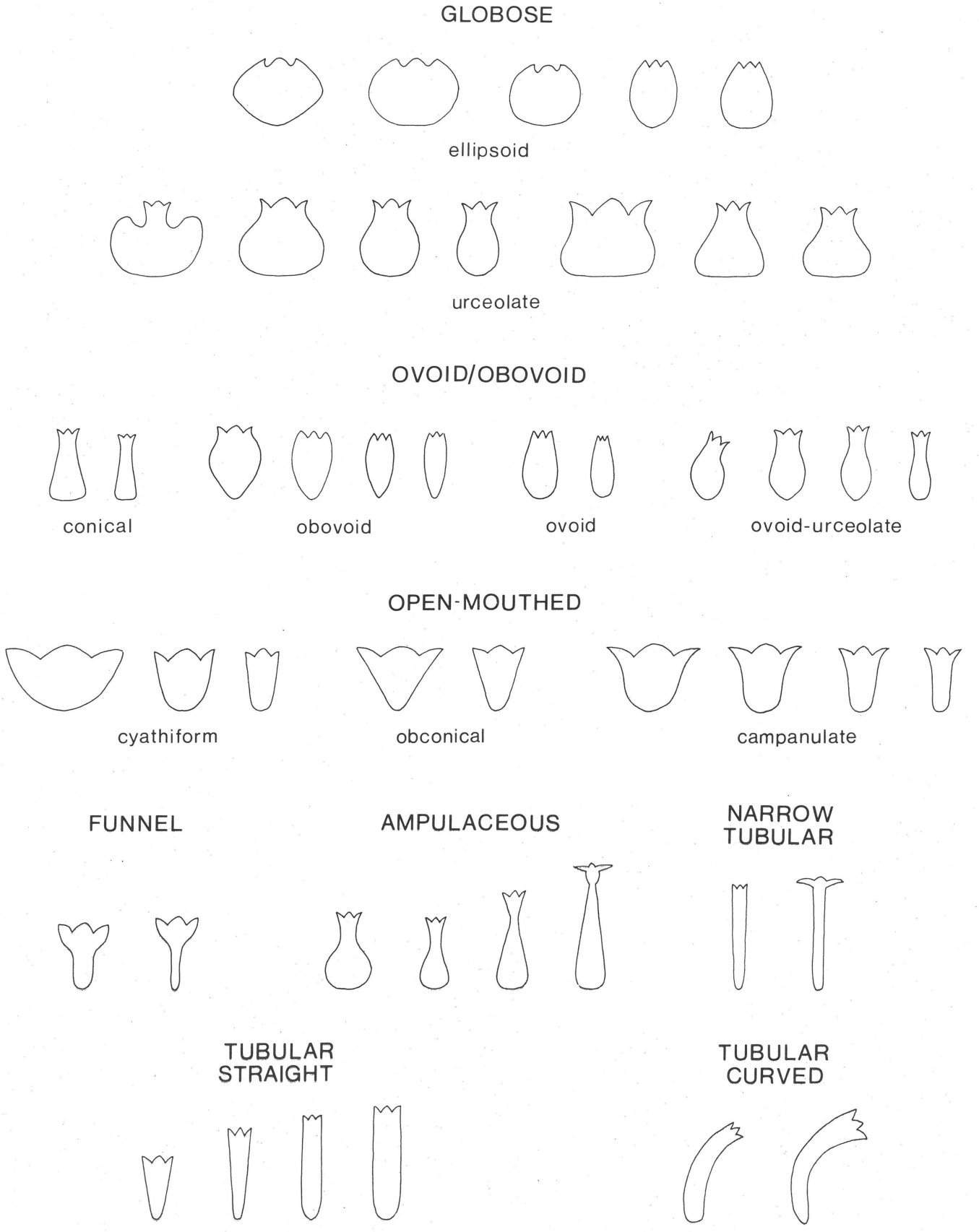

Figure 2 The diversity of *Erica* corolla morphology and the morphological groupings used in this study. The shapes are not drawn to the same scale, the lower groups being on average much larger than the upper groups. Adapted from Baker & Oliver (1967).

Anemophily

Wind pollination in *Erica* was not recorded by either Marloth (1932) or Vogel (1954). However, 5% of *Erica* species (sections Chlorocodon and Arsace) in the south-western Cape conform to the wind-pollination syndrome. The syndrome is restricted to three flower shapes (Table 1): globose, ovoid and open-mouthed. The major observable differences between insect-pollinated and wind-pollinated *Erica* species are the large cyathiform to peltate stigmas of the latter class, and the absence of conspicuous nectaries between the anther filaments

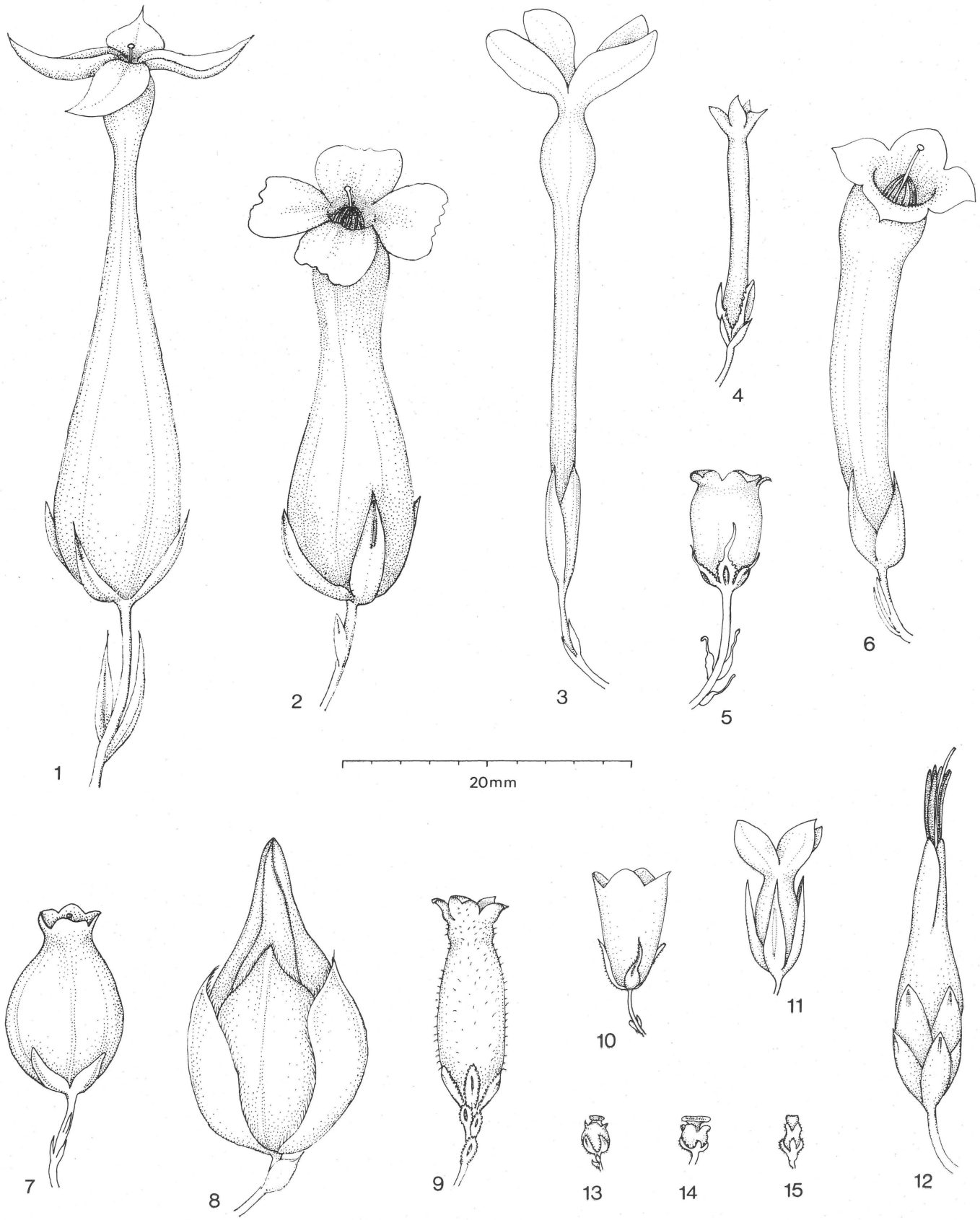

Figure 3 Examples of different pollination syndromes in *Erica* species. (1) *E. junonia* (LPF — long proboscid fly); (2) *E. aristata* (LPF); (3) *E. jasminiflora* (LPF); (4) *E. cylindrica* (insect — moth); (5) *E. lananthera* (insect); (6) *E. vestita* (bird); (6) *E. atrovinosa* (insect); (7) *E. lanuginosa* (closed flower — insect?); (8) *E. cristata* (LPF); (10) *E. heleogena* (insect); (11) *E. fastigiata* (LPF); (12) *E. coccinea* (bird); (13) *E. hispidula* (wind). Wind pollination syndrome in (14) *Philippia procaviana* and (15) *Scyphogyne urceolata*.

Table 1 The number of species according to principal pollination syndromes in sections of the genus *Erica* (426 spp.) in the south-western Cape

Subgenus	Section	Wind	Insect*	Bird
Syringodea	Gigandra, Didymanthera, Dasyanthes, Bactridium			14
	Pleurocallis		1	25
	Evanthe		1	27
	Chona		1	
Stellanthe	Euryloma		17 (15)	
	Ceramus		5 (3)	
	Callista		14 (8)	
	Platyspora		2	
	Myra		4 (4)	
Euerica	Ephebus, Desmia, Hermes, Leptodendron, Pachysa, Pseuderemia, Polydesmia, Pyronium		114	
	Ceramia	1	26	
	Gypsocallis	1	7	
	Orophanes	1	27	
	Chlorocodon	2		
	Arsace	13	2	
Chlamydanthe	Chromostegia, Amphodea, Oxyloma, Geissostegia, Eriodesmia, Eurystegia, Trigemma		57	
	Elytrostegia	1	3	
	Lamprotus		24 (1)	
Platystoma	Melastemon, Eurystoma, Gamochlamys		28	
	Polycodon	2	6	

*Long-proboscid fly (LPF) pollinated species (rhinomyiophilous) in parentheses

at the base of the ovary (Figure 4). The frequency of each floral shape among wind-pollinated species is similar to that occurring in the insect-pollination class (Table 2). Thus, the flowers of wind-pollinated *Erica* species are small versions of those of insect-pollinated species, suggesting that wind-pollinated species are derived from insect-pollinated species.

Most of the more specialized, small-flowered, wind-pollinated species occur within the minor genera *Philippia* Klotzsch, *Salaxis* Salisb., *Coccosperma* Klotzsch, *Scyphogyne* Brongn. and *Nagelocarpus* Bullock. (Representative examples of these species, *Philippia procaviana* E.G.H. Oliver and *Scyphogyne urceolata* (Klotzsch) Benth., are shown in Figures 3 & 4.) *Philippia*, as a genus separate from *Erica*, may not be upheld in work at present being undertaken (E.G.H. Oliver unpubl.). The incorporation of the nine south-western Cape species into *Erica* would increase the overall proportion of wind-pollinated species in the genus to about 11%.

The paucity of wind-pollinated *Erica* species contrasts strongly with the high incidence of wind pollination in members of the Restionaceae and Cyperaceae (pers. obs.) which form the dominant grass-like element in Mountain Fynbos vegetation. However, the incidence of wind pollination decreases markedly in the shrub layer (occurring in some minor genera of the Ericoideae, as mentioned above, a few species of *Erica* and sporadically in other non-ericaceous genera such as *Cliffortia*) and is largely absent in the overstorey, occurring only in a few genera (e.g. *Widdringtonia* and some species of *Leucadendron*) (pers. obs.; Williams 1972). This decrease in wind pollination with increasing complexity of fynbos vegetation structure may be a function of decreasing population dominance in higher strata, as opposed to the situation in some other vegetation types (e.g. deciduous or coniferous forest) (Ostler & Harper 1978; Whitehead 1969). The species of *Erica* which forms the most dense stands and is the dominant plant in the communities in which it occurs, is *E. hispidula* which is wind-pollinated (pers. obs.).

Ornithophily

Bird pollination in *Erica* has been described by Scott-Elliot (1890), Marloth (1932) and Vogel (1954), and is represented by 15% of *Erica* species in the south-western Cape (Table 2). The bird-pollination syndrome in the genus consists of two main flower shapes: tubular straight, and tubular curved, flowers (Table 2). Species having tubular straight flowers can be divided, on the basis of anther morphology, into 'brush-flower' and 'tube-flower' classes (Figure 3) (Vogel 1954; Rebelo *et al.* 1984). The brush-flower species (sections Gigandra and Didymanthera) have exserted stamens which form a tube around the style, effectively doubling the length of the flower. The anthers are joined at their elongate pores into an 'anther ring' which must be broken in order to gain access to the perianth tube. The anthers, when separating, dust pollen

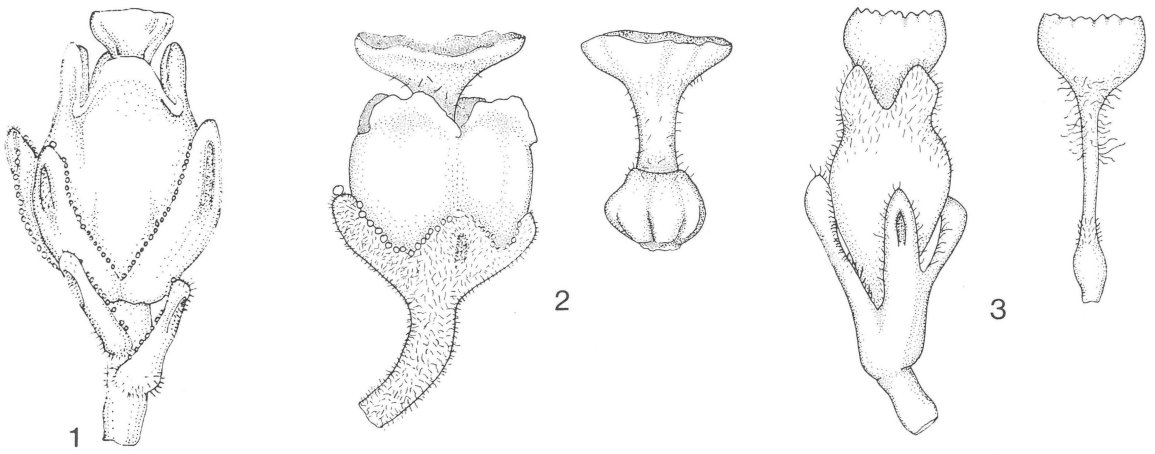

Figure 4 Floral details of anemophilous species of Ericaceae. (1) *Erica hispidula*, ×15; (2) *Philippia procaviana*, flower and gynoecium showing stigma, ×15; (3) *Scyphogyne urceolata*, flower and gynoecium showing stigma, ×18.

Table 2 The number of species grouped according to principal corolla morphology (see Figure 2) and pollination syndromes in the genus *Erica* (426 spp.) in the south-western Cape. (The numbers in parentheses represent the percentage occurrence of species)

Pollination syndrome	Corolla shape								Total number of species
	Globose	Ovoid-Obovoid	Open-mouthed	Ampullaceous	Funnel	Narrow tubular	Tubular straight	Tubular curved	
Anemophily	2 (9%)	6 (29%)	13 (62%)						21
Entomophily*	44 (14%)	94 (31%)	148 (48%)	18 (6%)		3 (1%)	1 (0%)		308
Rhinomyiophily		10 (32%)		17 (55%)	3 (10%)	1 (3%)			31
Ornithophily		1 (2%)	3 (4%)	4 (6%)			48 (73%)	10 (15%)	66

*Excluding long-proboscid fly (LPF) pollinated species (rhinomyiophilous)

onto the beaks and foreheads of probing birds. The distal style and stigma protrude from the anther ring and collect pollen from the probing bird. Tube-flower species have their anthers situated at the mouth of the perianth tube or just inside it (sections Pleurocallis, Evanthe, Dasyanthes and Bactridium) and comprise the majority (68%) of bird-pollinated *Erica* species. In these species the anther ring breaks when probed by a bird, depositing pollen on its beak and forehead. Fifteen per cent of bird-pollinated *Erica* species have strongly curved tubular flowers, matching the curve of the beak of the major bird pollinator, the Orange-breasted Sunbird *Nectarinia violacea*.

The predominant flower colours among bird-pollinated *Erica* species are red, pink and white, with red, orange, yellow and green flowers being relatively well represented compared with non-bird-pollinated species (Rebelo & Siegfried 1985). There is also a high incidence of bicoloured (and tricoloured) flowers among the bird-pollinated species. A prominent feature in many bird-pollinated *Erica* species is the high incidence of colour polymorphism, with almost 50% of bird-pollinated *Erica* species having two or more flower colour forms. This contrasts with a much lower proportion of colour polymorphism in insect and wind-pollinated species (Rebelo & Siegfried 1985).

Because the mass of avian pollinators is far greater than that of insect pollinators, bird-pollinated *Erica* species tend to have much thicker stems than insect or wind-pollinated *Erica* species (Siegfried, Rebelo & Prŷs-Jones 1985).

The corolla tube is externally very viscid in some bird-pollinated *Erica* species (e.g. *E. fascicularis, E. massonii, E. tenax* and *E. thomae*.); probably to prevent nectar and pollen thieving by insects (including honey bees, *Apis mellifera capensis*). They become entangled on the corolla and are gleaned by visiting nectarivorous birds (pers. obs.). Seed set in these species appears to be very low.

The low species diversity of avian pollinators of *Erica* in the south-western Cape contrasts strongly with avian pollinator:plant species ratios found in other geographical areas (Rebelo *et al.* 1984). This, together with the relatively uniform shape of bird-pollinated flowers in the genus, raises the problem of how pollen is segregated between co-occurring bird-pollinated *Erica* species in the south-western Cape.

Entomophily

The majority (80%) of *Erica* species are insect-pollinated (Table 2). Nine per cent of *Erica* species are rhinomyiophilous and are visited by flies with elongated proboscises which are used for sucking nectar, such as those of the families Tabaniidae, Bombyliidae and Nemestrinidae (Vogel 1954). These hovering dipterans visit flowers which are both long (matching in length the flies' mouthparts) (Vogel 1954; pers. obs.) and ampullaceous (Figures 2 & 3). The flowers differ from those of bird-pollinated species in that the orifice is very small (< 2 mm Ø) and the corolla lobes are large, star-shaped and spreading. The flowers are orientated to point upwards, between the vertical and the horizontal, and a fly obtains nectar by hovering over the flower until its proboscis is positioned correctly; it then inserts the proboscis into the corolla tube by flying towards the flower. The flies may hover or sometimes hang, using their forelegs, on the corolla lobes (which in *E. aristata* are orientated to support the flies' legs) while sucking nectar.

The section Euryloma (and possibly most of the subgenus *Stellanthe*) has the most distinct examples of LPF-pollinated flowers (Figure 3; Table 1), although the section also includes some bird-pollinated species which have flowers with larger orifices (e.g. *E. ventricosa*). Many LPF-pollinated species are robbed by birds which slit the bases of the flowers to gain access to the nectar. LPF-pollinated species grade with moth-pollinated species, the latter having larger corolla lobes and strong nocturnal scents (Vogel 1954). However, relatively few species of *Erica* are scented (e.g. *E. cylindrica* and *E. denticulata* in this group) and many of the species designated by Vogel (op. cit.) as moth-pollinated are visited by long proboscid dipterans. Viscid corollas also occur in LPF-pollinated *Erica* species (e.g. *E. aristata, E. retorta* and *E. jasminiflora*) and one species (*E. junonia*) has a slippery waxy corolla which presumably hinders nectar thieving by insects which tend to bite through the corolla base. Butterfly visits to putatively LPF-pollinated species have never been observed, and butterflies are probably excluded by the orientation of the flowers, the lack of suitable landing platforms and the viscid-waxy nature of the corolla.

Categorization of the non-LPF-pollinated insect-pollinated *Erica* species is complex. The cyathiform, campanulate and obconical flowers (Figures 2 & 3) (the bell or funnel blossoms of Faegri & Van der Pijl 1979) theoretically do not restrict the access of insects to either the nectar or pollen. These flowers occur sporadically in all the subgenera, but especially in *Platystoma*, and represent 44% of the insect-pollinated species (Table 2). These species are probably largely mellitophilous (bee-pollinated), although some species are visited by dipterans (myiophily) as well. Although small beetles visit *Erica* flowers occasionally, their importance as pollinators in the genus is unknown.

The remaining insect-pollinated species (41%) have globose, obovoid, urceolate or conical flowers (Figures 2 & 3) with the anthers either exserted or inside the corolla tube. The species with exserted anthers are probably mainly bee-pollinated. They tend to have no anther appendages (Palser & Murty 1967) and provide both pollen and nectar for pollinators. Species with the anthers (often with elaborate awns)

positioned behind the small mouth of the flower provide nectar exclusively and are probably predominantly LPF and butterfly-pollinated.

The majority of flower-visiting insects seen on Ericaceae feed on the strongly scented minor genera (e.g. *Blaeria* L.) and on the few *Erica* species with marked honey scents (*E. caffra*, *E. parviflora*). These species tend to be visited by a large variety of bees and flies, most of which carry pollen of several plant families and genera (Robertson 1980). *Apis mellifera capensis* is apparently the only bee where workers largely confine their visits to a single species of *Erica* (Robertson 1980). It, however, is scarce owing to a lack of suitable nesting sites in its habitats (P. Worsley-Worswick, pers. comm.).

Problems were encountered when assigning putative pollinators to some species of the section Eurystegia (*E. halicacaba* and *E. lanuginosa*). The corolla lobes of these large flowered species tend to remain adpressed to one another for the life of the flower and, therefore, form closed flowers (*sensu* Faegri & Van der Pijl 1979). In *E. lanuginosa* (Figure 3) the corolla lobes are hinged and snap closed after being forcefully opened. The possibility of visitation by birds or large hymenopterans needs to be investigated. The bases of flowers of specimens of these species in the National Botanic Gardens at Kirstenbosch are frequently damaged by bees which chew holes through the petals to gain access to the copious nectar. In this they resemble the non-sticky bird-pollinated *Erica* species which are often damaged by bees (pers. obs.).

The richness of floral species in the south-western Cape (Goldblatt 1978; Oliver *et al.* 1983) is paralleled by a richness of insect taxa relative to neighbouring regions. Among lepidopterans, the region is particularly rich in Satyridae and Lycaenidae (Pinhey 1978). The region also has a rich hymenopteran fauna, with many endemic species (Prins 1978), and the 'biome of the Cape proper' is characterized by many endemic coleopteran species and genera (Endrödy-Younga 1978). The dipterans parallel these trends: 'it is the consequent richness in numbers of species, rather than the uniqueness of taxa, which is the outstanding feature of the dipterous fauna of the Cape' (Bowden 1978). The south-western Cape is the richer of the two centres of high dipteran diversity in southern Africa. Dipteran richness is accounted for most markedly by species with anthophile adults, but 'relations between Diptera and flowers have not received the attention they merit' (Bowden 1978).

Conclusions

The incidence of wind pollination is low in the genus *Erica*. This is consistent with the species richness of the Cape Floral Kingdom. Wind pollination, because of its broadcast random methods of pollen transfer, is limited to species which are numerically dominant in the vegetation, and also limits the numbers of closely related co-occurring species.

Insect-pollinated *Erica* species have diverse pollination mechanisms. This resembles tropical pollination systems more closely than those of temperate regions. The high incidence of the specialized syndrome of LPF-pollination may be paralleled by a similar diversity of other insect-pollination syndromes. Despite the richness of insect-pollinated *Erica* species in the south-western Cape, most of the species which are visited regularly by insects appear to be visited by representatives of a wide range of families, many of which are potentially effective pollinators. Competition for pollinators may account for the low rates of plant visitation observed in the species-rich plant communities of the south-western Cape, especially since insect biomass is lower than that typical of other temperate regions (Schlettwein 1984). Further studies are required to delimit these syndromes, and to determine the apparently dynamic nature of insect pollination and pollen flow in *Erica*.

The occurrence of a single major avian pollinator (the Orange-breasted Sunbird) for 15% of the local *Erica* species is anomalous, but differs from wind pollination in that birds are more selective pollen vectors and tend to utilize species' patches by establishing territories at rich nectar sources, thus segregating pollen flow. Virtually nothing is known about avian nectarivore population dynamics in the south-western Cape. Yet, this information is crucial to an understanding of the ecology of many fynbos species, since avian pollinators comprise 50% of the avian biomass in Mountain Fynbos (Siegfried 1983). The low avian pollinator:ornithophilous *Erica* species ratio suggests that many of these species evolved subsequent to their avian pollinator, rather than having co-evolved contemporaneously, as appears to have happened in tropical ecosystems (Stiles 1981).

Acknowledgements

We thank Elisabeth Brown, Sue Frost and the staff of the Bolus Herbarium at the University of Cape Town for their assistance. Robert Prŷs-Jones and two anonymous referees made useful comments on the manuscript. The South African Council for Scientific and Industrial Research, through its Fynbos Biome Project, and the University of Cape Town provided financial support.

References

ANDERSON, R.H., BUYS, B. & JOHANNSMEIER, M.F. 1983. Beekeeping in South Africa. Bull. no. 394. Dept Agriculture, Pretoria.

BAKER, H.A. & OLIVER, E.G.H. 1967. Ericas in southern Africa. Purnell, Cape Town.

BOND, P. & GOLDBLATT, P. 1984. Plants of the Cape Flora, a descriptive catalogue. *Jl S. Afr. Bot.* Suppl. Vol. 14.

BOWDEN, J. 1978. Diptera. In: Biogeography and Ecology of Southern Africa, ed. Werger, M.J.A., Junk, The Hague.

COLLINS, B.G. 1983. Pollination of *Mimetes hirtus* (Proteaceae) by Cape Sugarbirds and Orange-breasted Sunbirds. *Jl S. Afr. Bot.* 49: 125 – 142.

DULFER, H. 1965. Revision der südafrikanischen Arten der Gattung *Erica* L. 2 Teil. *Ann. Naturhistor. Mus. Wien* 68: 25 – 177.

ENDRÖDY-YOUNGA, S. 1978. Coleoptera. In: Biogeography and Ecology of Southern Africa, ed. Werger, M.J.A., Junk, The Hague.

FAEGRI, K. & VAN DER PIJL, L. 1979. The principles of pollination ecology, 3rd edn, Pergammon, Oxford.

GIBBS RUSSELL, G.E. 1984. List of species of southern African plants. *Mem. bot. Surv. S. Afr.* No. 48. 144 pp.

GOLDBLATT, P. 1978. An analysis of the flora of southern Africa: Its characteristics, relationships and origins. *Ann. Mo. bot. Gdn* 65: 369 – 436.

HAGERUP, O. 1950. Thrips pollination in *Calluna*. *Det. Kgl. Dansk. Vidensk. Selbs. Biol. Meddel.* 18(4): 1 – 16.

HAGERUP, O. 1951. Pollination in the Faroes — in spite of rain and poverty in insects. *Det. Kgl. Dansk. Vidensk. Selbs. Biol. Meddel.* 18(15): 1 – 48.

HAGERUP, E. & HAGERUP, O. 1953. Thrips pollination of *Erica tetralix*. *New Phytol.* 52: 1 – 7.

HERRMANN, J.M. 1985. Insect pollination of some *Erica* species in the south-western Cape. *Veld & Flora* 71: 57 – 60.

KNUTH, P. 1906 – 1909. Handbook of flower pollination. 3 Vols. Oxford University Press, Oxford.

LEWIS, T. 1973. Thrips. Their biology, ecology and economic importance. Academic Press, London.

MARLOTH, R. 1932. The flora of South Africa, with a synopsis of the South African genera of phanerogramous plants. Vol. III, Sect. 1. Darter Bros, Cape Town.

OLIVER, E.G.H., LINDER, H.P. & ROURKE, J.R. 1983. Geographical distribution of present day Cape taxa and their phytogeographical significance. *Bothalia* 14: 427 – 440.
OSTLER, W.K. & HARPER, K.T. 1978. Floral ecology in relation to plant species diversity in the Wasatch Mountains of Utah and Idaho. *Ecology* 59: 848 – 861.
PALSER, B.F. & MURTY, Y.S. 1967. Studies of floral morphology in the Ericales. VIII. Organography and vascular anatomy in *Erica*. *Bull. Torrey Bot. Club* 94: 243 – 320.
PINHEY, E. 1978. Lepidoptera. In: Biogeography and Ecology of Southern Africa, ed. Werger, M.J.A., Junk, The Hague.
PRINS, A.J. 1978. Hymenoptera. In: Biogeography and Ecology of Southern Africa, ed. Werger, M.J.A., Junk, The Hague.
REBELO, A.G. & SIEGFRIED, W.R. 1985. Colour and size of flowers in relation to pollination of *Erica* species. *Oecologia* 65: 584 – 590.
REBELO, A.G. & SIEGFRIED, W.R. 1985. Flower colour polymorphism in the genus *Erica*. *Oecologica*
ROBERTSON, H.G. 1980. Pollination of selected *Erica* species in the Cape Fynbos. Unpublished postgraduate project, University of Cape Town.
SCHLETTWEIN, C.H.G. 1984. Comparison of insect biomass and community structure between fynbos sites of different ages after fire with particular reference to ants, leafhoppers and grasshoppers. Unpublished MSc. thesis, University of Stellenbosch.
SCOTT-ELLIOT, F. 1890. Ornithophilous plants in South Africa. *Ann. Bot.* 4: 265 – 280.
STILES, F.G. 1981. Geographical aspects of bird-flower co-evolution, with particular reference to Central America. *Ann. Mo. bot. Gdn* 68: 323 – 351.
SIEGFRIED, W.R. 1983. Trophic structure of some communities of fynbos birds. *Jl S. Afr. Bot.* 49: 1 – 43.
SIEGFRIED, W.R., REBELO, A.G. & PRŶS-JONES, R.P. 1985. Stem thickness in *Erica* species. *Oikos*: in press.
VOGEL, S. 1954. Blutenbiologische typen als elemente der Sippengleiderung. Gustav Fischer Verlag, Jena.
WHITEHEAD, D.R. 1969. Wind pollination in the Angiosperms: Evolutionary and environmental considerations. *Evolution* 23: 28 – 35.
WILLIAMS, I.J.M. 1972. A revision of the genus *Leucadendron* (Proteaceae). *Contr. Bolus Herb.* 3: 1 – 425.

Appendix 1 Putative principal pollination syndromes and shape of corollas for 426 *Erica* species in the south-western Cape. Nomenclature follows Gibbs Russell (1984) and numeration follows Dulfer (1965)

	Section	Species	Polli-nation	Corolla shape
1.	Gigandra	*coccinea* L.	Bird	Tubular straight
3.		*lineata* Benth.	Bird	Tubular straight
4.		*breviflora* Dulfer	Bird	Tubular straight
5.		*plukenetii* L.	Bird	Tubular straight
6.	Didyman-thera	*monadelphia* Andr.	Bird	Tubular straight
7.		*banksia* Andr.	Bird	Tubular straight
7.a		*comptonii* Salter	Bird	Tubular straight
8.a		*leucosiphon* L. Bol.	Bird	Tubular straight
12.	Pleuro-callis	*mammosa* L.	Bird	Tubular straight
16.		*sessiliflora* L.f.	Bird	Tubular curved
17.		*filipendula* Benth.	Bird	Tubular straight
17.a		*globulifera* Dulfer	Insect	Ovoid-Obovoid
19.		*grandiflora* L.f.	Bird	Tubular straight
20.		*longisepala* Guth. & Bol.	Bird	Tubular straight
21.		*hibbertia* Andr.	Bird	Tubular straight
21.a		*tenax* L. Bol.	Bird	Tubular curved
21.b		*thomae* L. Bol.	Bird	Tubular curved
21.c		*porteri* Compton	Bird	Tubular curved
22.		*phylicifolia* Salisb.	Bird	Tubular curved
22.a		*nevillei* L. Bol.	Bird	Tubular curved
22.b		*quadrisulcata* L. Bol.	Bird	Tubular curved
23.		*abietina* L.	Bird	Tubular straight
24.		*conica* Lodd.	Bird	Tubular straight
25.		*pinea* Thunb.	Bird	Tubular straight
27.		*annectens* Guth. & Bol.	Bird	Tubular straight
28.		*regia* Bartl.	Bird	Tubular straight
29.		*casta* Guth. & Bol.	Bird	Tubular straight
30.		*mariae* Guth. & Bol.	Bird	Tubular straight
31.		*vestita* Thunb.	Bird	Tubular straight
33.		*filamentosa* Andr.	Bird	Tubular straight
34.		*longifolia* Ait.	Bird	Tubular straight
34.a		*gallorum* L. Bol.	Bird	Open-mouthed
35.		*onosmiflora* Salisb.	Bird	Tubular straight
+		*vallis-aranearum* E.G.H. Oliver	Bird	Tubular straight
36.	Evanthe	*patersonia* Andr.	Bird	Tubular straight
37.		*sacciflora* Salisb.	Bird	Tubular straight
38.		*foliacea* Andr.	Bird	Ovoid-Obovoid
39.		*nana* Salisb.	Bird	Tubular straight
40.		*xanthina* Guth. & Bol.	Bird	Open-mouthed
41.		*maximilianii* Guth. & Bol.	Bird	Open-mouthed
44.		*bibax* Salisb.	Bird	Tubular straight
45.		*curviflora* L.	Bird	Tubular curved
48.		*conspicua* Soland.	Bird	Tubular straight
50.		*xerophila* H. Bol.	Bird	Tubular straight
53.		*discolor* Andr.	Bird	Tubular curved
56.		*serratifolia* Andr.	Bird	Tubular straight
57.		*macowanii* Cufino	Bird	Tubular straight
57.a		*leucotrachela* H.A. Bak.	Bird	Tubular straight
57.b		*cremea* Dulfer	Bird	Tubular straight
58.		*versicolor* Andr.	Bird	Tubular straight
59.		*berzelioides* Guth. & Bol.	Bird	Tubular straight
61.a		*pyrantha* L. Bol.	Bird	Tubular straight
62.		*perspicua* Wendl.	Bird	Tubular straight
62.a		*octonaria* L. Bol.	Bird	Tubular straight
62.b		*dulcis* L. Bol.	Insect	Globose
63.		*colorans* Andr.	Bird	Tubular straight
64.		*verticillata* Berg.	Bird	Tubular straight
66.		*cruenta* Soland.	Bird	Tubular straight
66.a		*pillansii* H. Bol.	Bird	Tubular straight
66.b		*fervida* L. Bol.	Bird	Tubular straight
68.		*haematosiphon* Guth. & Bol.	Bird	Tubular straight
70.		*brachialis* Salisb.	Bird	Tubular straight
74.	Dasy-anthes	*doliiformis* Salisb.	Bird	Ampullaceous
75.		*tumida* Ker-Gawl.	Bird	Tubular straight
75.a		*cameronii* L. Bol.	Bird	Ampullaceous
77.		*cerinthoides* L.	Bird	Ampullaceous
78.	Chona	*embothriifolia* Salisb.	Insect	Ovoid-Obovoid
79.	Bactri-dium	*fascicularis* L.f.	Bird	Tubular curved
80.		*massonii* L.f.	Bird	Ampullaceous
81.	Eury-loma	*gysbertii* Guth. & Bol.	Insect*	Ovoid-Obovoid
81.a		*intonsa* L. Bol.	Insect*	Ovoid-Obovoid
81.b		*cygnea* Salter	Insect*	Ovoid-Obovoid
82.		*squarrosa* Salisb.	Insect*	Ampullaceous
83.		*aristata* Andr.	Insect*	Ampullaceous
84.		*retorta* Montin	Insect*	Ampullaceous
86.		*jasminiflora* Salisb.	Insect*	Narrow-tubular
87.		*junonia* H. Bol.	Insect*	Ampullaceous
88.		*shannonea* Andr.	Insect*	Ampullaceous
89.		*ampullacea* Curt.	Insect*	Ampullaceous
90.		*irbyana* Andr.	Insect	Ampullaceous
91.		*curvifolia* Salisb.	Insect*	Ovoid-Obovoid
92.		*cristata* Dulfer	Insect*	Ovoid-Obovoid
93.		*trichroma* Benth.	Insect*	Ovoid-Obovoid
94.		*tubercularis* Salisb.	Insect*	Ovoid-Obovoid
95.		*rhodopis* (H. Bol.) H. Bol.	Insect*	Ovoid-Obovoid
95.a		*lananthera* L. Bol.	Insect	Open-mouthed
97.	Ceramus	*savilea* Andr.	Insect*	Ampullaceous
99.		*inflata* Thunb.	Insect*	Ovoid-Obovoid
100.		*ventricosa* Thunb.	Insect*	Ampullaceous
+		*atrovinosa* E.G.H. Oliver	Insect	Globose
+		*toringbergensis* H.A. Bak.	Insect	Ovoid-Obovoid
101.	Callista	*lawsonia* Andr.	Insect	Narrow-tubular
102.		*infundibuliformis* Andr.	Insect	Narrow-tubular
103.		*cylindrica* Thunb.	Insect	Narrow-tubular
104.		*fastigiata* L.	Insect*	Funnel-shaped
105.		*transparens* Berg.	Insect*	Ampullaceous
106.		*vallis-gratiae* Guth. & Bol.	Insect*	Funnel-shaped

Appendix 1 continued

	Section	Species	Polli-nation	Corolla shape
108.		*walkeria* Andr.	Insect*	Funnel-shaped
109.		*daphniflora* Salisb.	Insect*	Ovoid-Obovoid
110.		*pellucida* Soland. ex Salisb.	Insect	Ampullaceous
111.		*denticulata* L.	Insect	Ovoid-Obovoid
+		*glabripes* L. Bol.	Insect*	Ampullaceous
+		*hendricksei* H.A. Bak.	Insect	Ovoid-Obovoid
+		*turrisbabylonica* H.A. Bak.	Insect*	Ampullaceous
+		*vinacea* L. Bol.	Insect*	Ampullaceous
115.	Platy-spora	*macilenta* Guth. & Bol.	Insect	Ampullaceous
118.		*glandulifera* Klotzsch	Insect	Globose
119.	Myra	*irrorata* Guth. & Bol.	Insect*	Ampullaceous
120.		*rufescens* Klotzsch	Insect*	Ampullaceous
121.		*glutinosa* Berg.	Insect*	Ampullaceous
122.		*armata* Klotzsch ex Benth.	Insect*	Ampullaceous
124.	Ephebus	*peziza* Lodd.	Insect	Open-mouthed
125.		*ovina* Klotzsch	Insect	Ovoid-Obovoid
126.		*tomentosa* Salisb.	Insect	Open-mouthed
127.		*pubigera* Salisb.	Insect	Ovoid-Obovoid
128.		*constantia* Nois. ex Benth.	Insect	Ovoid-Obovoid
129.		*albescens* Klotzsch ex Benth.	Insect	Open-mouthed
130.		*oxyandra* Guth. & Bol.	Insect	Ovoid-Obovoid
133.a		*hippurus* Compton	Insect	Ovoid-Obovoid
134.		*aemula* Guth. & Bol.	Insect	Open-mouthed
136.		*sicifolia* Salisb.	Insect	Open-mouthed
137.		*podophylla* Benth.	Insect	Open-mouthed
139.		*propendens* Andr.	Insect	Open-mouthed
140.		*pyramidalis* Soland.	Insect	Open-mouthed
141.		*chrysocodon* Guth. & Bol.	Insect	Open-mouthed
142.		*trichophora* Benth.	Insect	Open-mouthed
143.		*setulosa* Benth.	Insect	Open-mouthed
144.		*canescens* Wendl.	Insect	Open-mouthed
145.		*distorta* Bartl.	Insect	Open-mouthed
145.a		*haematocodon* Salter	Insect	Open-mouthed
146.		*caterviflora* Salisb.	Insect	Ovoid-Obovoid
147.		*parviflora* L.	Insect	Ovoid-Obovoid
148.		*intervallaris* Salisb.	Insect	Open-mouthed
149.		*cyrilliflora* Salisb.	Insect	Ampullaceous
149.a		*fontana* L. Bol.	Insect	Open-mouthed
149.b		*heleogena* Salter	Insect	Open-mouthed
149.c		*paludicola* L. Bol.	Insect	Open-mouthed
149.d		*limosa* L. Bol.	Insect	Open-mouthed
149.e		*salteri* L. Bol.	Insect	Open-mouthed
151.		*turgida* Salisb.	Insect	Open-mouthed
153.		*oresigena* H. Bol.	Insect	Ovoid-Obovoid
156.		*hirtiflora* Curt.	Insect	Globose
156.a		*bolusiae* Salter	Insect	Open-mouthed
157.		*mollis* Andr.	Insect	Globose
158.		*ribisaria* Guth. & Bol.	Insect	Ovoid-Obovoid
159.		*oophylla* Benth.	Insect	Globose
160.		*trichadenia* H. Bol.	Insect	Open-mouthed
161.		*eriocodon* H. Bol.	Insect	Open-mouthed
163.		*perlata* Sincl.	Insect	Globose
164.		*pannosa* Salisb.	Insect	Ovoid-Obovoid
165.		*fausta* Salisb.	Insect	Open-mouthed
166.		*setosa* Bartl.	Insect	Open-mouthed
168.		*lerouxiae* H. Bol.	Insect	Open-mouthed
169.		*caffra* L.	Insect	Open-mouthed
170.		*pubescens* L.	Insect	Globose
171.		*hirta* Thunb.	Insect	Globose
173.		*sphaeroidea* Dulfer	Insect	Globose
173.a		*tradouwensis* Compton	Insect	Ovoid-Obovoid
174.		*marifolia* Soland.	Insect	Ovoid-Obovoid
175.		*argyraea* Guth. & Bol.	Insect	Globose
+		*phillipsii* L. Bol.	Insect	Globose
176.	Ceramia	*cymosa* E. Mey. ex Benth.	Insect	Open-mouthed
177.		*oreophila* Guth. & Bol.	Insect	Open-mouthed
178.		*planifolia* L.	Insect	Open-mouthed
180.		*cryptanthera* Guth. & Bol.	Insect	Open-mouthed
181.		*tenuipes* Guth. & Bol.	Insect	Open-mouthed

Appendix 1 continued

	Section	Species	Polli-nation	Corolla shape
182.		*physophylla* Benth.	Insect	Open-mouthed
182.a		*utriculosa* L. Bol.	Insect	Open-mouthed
183.		*oxycoccifolia* Salisb.	Insect	Open-mouthed
184.		*tenuicaulis* Klotzsch ex Benth.	Insect	Open-mouthed
185.		*myriocodon* Guth. & Bol.	Insect	Open-mouthed
186.a		*atropurpurea* Dulfer	Insect	Open-mouthed
187.		*leptoclada* v.Huerck & Muell.Arg.	Insect	Open-mouthed
187.a		*petrophila* L. Bol.	Insect	Open-mouthed
188.a		*cederbergensis* Compton	Insect	Open-mouthed
189.		*marlothii* H. Bol.	Insect	Ovoid-Obovoid
190.		*oligantha* Guth. & Bol.	Insect	Ovoid-Obovoid
192.		*thimifolia* Wendl.	Insect	Open-mouthed
192.a		*riparia* H.A. Bak.	Insect	Globose
193.		*filiformis* Salisb.	Insect	Open-mouthed
195.		*aspalathoides* Guth. & Bol.	Insect	Open-mouthed
196.		*mundii* Guth. & Bol.	Insect	Open-mouthed
197.		*strigosa* Soland.	Insect	Open-mouthed
199.		*permutata* Dulfer	Insect	Globose
201.		*flacca* E.Mey. ex Benth.	Insect	Ovoid-Obovoid
203.		*cordata* Andr.	Insect	Open-mouthed
206.		*macrophylla* Klotzsch ex Benth.	Insect	Ovoid-Obovoid
207.		*ocellata* Guth. & Bol.	Wind	Ovoid-Obovoid
208.	Desmia	*conferta* Andr.	Insect	Globose
209.		*polifolia* Salisb. ex Benth.	Insect	Ovoid-Obovoid
210.		*obtusata* Klotzsch ex Benth.	Insect	Open-mouthed
210.a		*oliveri* H.A. Bak.	Insect	Globose
+		*krugeri* E.G.H. Oliver	Insect	Open-mouthed
211.	Gypso-callis	*racemosa* Thunb.	Insect	Ovoid-Obovoid
212.		*aghillana* Guth. & Bol.	Insect	Globose
214.		*longipedunculata* Dulfer	Insect	Ovoid-Obovoid
215.		*rubiginosa* Dulfer	Wind	Open-mouthed
216.		*scytophylla* Guth. & Bol.	Insect	Ovoid-Obovoid
217.		*capillaris* Bartl.	Insect	Open-mouthed
217.a		*chonantha* Dulfer	Insect	Open-mouthed
218.		*nudiflora* L.	Insect	Open-mouthed
224.	Pyro-nium	*paniculata* L.	Insect	Open-mouthed
225.		*bicolor* Thunb.	Insect	Open-mouthed
226.		*diotiflora* Salisb.	Insect	Open-mouthed
229.		*parvula* Guth. & Bol.	Insect	Open-mouthed
231.		*brachysepala* Guth. & Bol.	Insect	Open-mouthed
233.	Oro-phanes	*pilulifera* L.	Insect	Ovoid-Obovoid
234.		*subulata* Wendl.	Insect	Ovoid-Obovoid
237.		*bergiana* L.	Insect	Globose
240.		*rubens* Thunb.	Insect	Globose
241.		*laeta* Bartl.	Insect	Open-mouthed
241.a		*capensis* Salter	Insect	Open-mouthed
242.		*turbiniflora* Salisb.	Insect	Open-mouthed
243.		*mauritanica* L.	Insect	Open-mouthed
244.		*sitiens* Klotzsch	Insect	Ovoid-Obovoid
244.a		*harmeriana* L. Bol.	Insect	Open-mouthed
244.b		*oreina* Dulfer	Insect	Open-mouthed
244.c		*mitchelliensis* Dulfer	Insect	Ovoid-Obovoid
245.		*blandfordia* Andr.	Insect	Ovoid-Obovoid
246.		*lateralis* Willd.	Insect	Globose
246.a		*autumnalis* L. Bol.	Insect	Open-mouthed
247.		*verecunda* Salisb.	Insect	Open-mouthed
248.		*tenella* Andr.	Insect	Ovoid-Obovoid
249.		*chionophylla* Guth. & Bol.	Wind	Ovoid-Obovoid
250.		*quadrangularis* Salisb.	Insect	Open-mouthed
251		*cyathiformis* Salisb.	Insect	Open-mouthed
253		*velitaris* Salisb.	Insect	Open-mouthed
254.a		*trichostigma* Salter	Insect	Globose
255.		*leucantha* Link.	Insect	Globose
256.		*subdivaricata* Berg.	Insect	Open-mouthed
256.a		*eburnea* Salter	Insect	Open-mouthed
257.		*margaritacea* Soland.	Insect	Open-mouthed
258.		*curvirostris* Salisb.	Insect	Open-mouthed
259.		*trichophylla* Benth.	Insect	Open-mouthed

Appendix 1 continued

	Section	Species	Pollination	Corolla shape
260.	Lepto-dendron	*rupicola* Klotzsch	Insect	Ovoid-Obovoid
261.a		*pauciovulata* H.A. Bak.	Insect	Open-mouthed
261.b		*elimensis* L. Bol.	Insect	Open-mouthed
264.		*vanhuerckii* Muell.Arg.	Insect	Open-mouthed
265.		*campanularis* Salisb.	Insect	Open-mouthed
265.a		*pageana* L. Bol.	Insect	Open-mouthed
265.c		*plena* L. Bol.	Insect	Open-mouthed
267.		*polycoma* Benth.	Insect	Open-mouthed
268.		*virginalis* Klotzsch	Insect	Open-mouthed
269.	Pachysa	*multumbellifera* Berg.	Insect	Globose
270.		*crenata* E. Mey. ex Benth.	Insect	Ovoid-Obovoid
271.		*macra* Guth. & Bol.	Insect	Ovoid-Obovoid
273.		*spectabilis* Klotzsch ex Benth.	Insect	Globose
277.		*nubigena* H. Bol.	Insect	Ovoid-Obovoid
277.a		*wittebergensis* Dulfer	Insect	Ovoid-Obovoid
281.		*glomiflora* Salisb.	Insect	Ovoid-Obovoid
282.		*physodes* L.	Insect	Ovoid-Obovoid
283.		*urna-viridis* H. Bol.	Insect	Ovoid-Obovoid
284.		*fairii* H. Bol.	Insect	Ovoid-Obovoid
285.		*oblongiflora* Benth.	Insect	Ovoid-Obovoid
286.		*odorata* Andr.	Insect	Globose
288.		*blenna* Salisb.	Insect	Ampullaceous
290.		*carduifolia* Salisb.	Insect	Open-mouthed
291.		*obliqua* Thunb.	Insect	Ovoid-Obovoid
+		*eustacei* L. Bol.	Insect	Globose
293.	Hermes	*empetrina* L.	Insect	Open-mouthed
294.		*pyxidiflora* Salisb.	Insect	Open-mouthed
295.		*amoena* Wendl.	Insect	Open-mouthed
296.		*dodii* Guth. & Bol.	Insect	Tubular straight
297.		*regerminans* L.	Insect	Globose
298.		*pulchella* Houtt.	Insect	Globose
299.		*longiaristata* Benth.	Insect	Ovoid-Obovoid
300.		*flavicoma* Benth.	Insect	Ampullaceous
301.		*parilis* Salisb.	Insect	Ovoid-Obovoid
302.		*viscaria* L.	Insect	Open-mouthed
303.		*axilliflora* Bartl.	Insect	Open-mouthed
303.a		*latiflora* L. Bol.	Insect	Open-mouthed
305.		*pulvinata* Guth. & Bol.	Insect	Ovoid-Obovoid
306.		*collina* Guth. & Bol.	Insect	Ovoid-Obovoid
306.a		*extrusa* Compton	Insect	Open-mouthed
431.a		*insolitanthera* H.A. Bak.	Insect	Ovoid-Obovoid
310.	Chloro-codon	*coarctata* Wendl.	Wind	Open-mouthed
311.		*curtophylla* Guth. & Bol.	Wind	Open-mouthed
315.	Arsace	*hispidula* L.	Wind	Globose
317.		*inops* H. Bol.	Wind	Globose
318.		*leucopelta* Tausch	Wind	Ovoid-Obovoid
319.		*maritima* Guth. & Bol.	Wind	Ovoid-Obovoid
320.		*salax* Salisb.	Wind	Ovoid-Obovoid
321.		*atricha* Dulfer	Wind	Open-mouthed
322.		*leptopus* Benth.	Insect	Open-mouthed
323.		*minutissima* Klotzsch ex Benth.	Wind	Open-mouthed
323.a		*philippioides* Compton	Wind	Open-mouthed
324.		*tenuis* Salisb.	Insect	Globose
325.		*crateriformis* Guth. & Bol.	Wind	Open-mouthed
327.		*copiosa* Wendl.	Wind	Open-mouthed
329.		*microcodon* Guth. & Bol.	Wind	Open-mouthed
329.a		*parvulisepala* H.A. Bak.	Wind	Open-mouthed
330.		*setacea* Andr.	Wind	Open-mouthed
331.	Pseude-remia	*cernua* Montin	Insect	Ovoid-Obovoid
332.		*maderi* Guth. & Bol.	Insect	Ovoid-Obovoid
332.a		*pudens* H.A. Bak.	Insect	Ovoid-Obovoid
333.		*sphaerocephala* Wendl. ex Benth.	Insect	Ovoid-Obovoid
337.		*oxysepala* Guth. & Bol.	Insect	Ovoid-Obovoid
337.a		*orculiflora* Dulfer	Insect	Ovoid-Obovoid
339.		*clavisepala* Guth. & Bol.	Insect	Ovoid-Obovoid
339a.		*acockii* Compton	Insect	Ovoid-Obovoid
340.	Poly-desmia	*bruniifolia* Salisb.	Insect	Open-mouthed
341.		*ustulescens* Guth. & Bol.	Insect	Ovoid-Obovoid
342.		*stylaris* Spreng.	Insect	Ovoid-Obovoid
343.		*turmalis* Salisb.	Insect	Ovoid-Obovoid
344.	Chromo-stegia	*eriophorus* Guth. & Bol.	Insect	Open-mouthed
345.		*involucrata* Klotzsch ex Benth.	Insect	Ovoid-Obovoid
346.		*senilis* Klotzsch ex Benth.	Insect	Ovoid-Obovoid
348.	Oxyloma	*genistifolia* Salisb.	Insect	Ovoid-Obovoid
349.		*cumuliflora* Salisb.	Insect	Ovoid-Obovoid
351.	Eriodes-mia	*villosa* Wendl.	Insect	Globose
352.		*bruniades* L.	Insect	Globose
353.		*capitata* L.	Insect	Globose
354.	Ampho-dea	*sexfaria* Ait.	Insect	Ovoid-Obovoid
355.		*spumosa* L.	Insect	Ovoid-Obovoid
356.		*amphigena* Guth. & Bol.	Insect	Ovoid-Obovoid
357.	Geisso-stegia	*desmantha* Benth.	Insect	Ovoid-Obovoid
359.		*aduncа* Benth.	Insect	Ovoid-Obovoid
361.		*chartacea* Guth. & Bol.	Insect	Ovoid-Obovoid
362.		*suffulta* Wendl. ex Benth.	Insect	Open-mouthed
363.		*pogonanthera* Bartl.	Insect	Ovoid-Obovoid
364.		*azaleifolia* Salisb.	Insect	Ovoid-Obovoid
365.		*sonderiana* Guth. & Bol.	Insect	Ovoid-Obovoid
365.a		*subimbricata* Compton	Insect	Open-mouthed
366.		*crassisepala* Benth.	Insect	Ovoid-Obovoid
367.		*guthriei* H. Bol.	Insect	Ovoid-Obovoid
368.		*placentiflora* Salisb.	Insect	Open-mouthed
369.		*imbricata* L.	Insect	Open-mouthed
370.		*triceps* Link.	Insect	Open-mouthed
371.		*penicilliformis* Salisb.	Insect	Open-mouthed
372.	Elytro-stegia	*lasciva* Salisb.	Wind	Ovoid-Obovoid
373.		*accomodata* Klotzsch ex Benth.	Insect	Open-mouthed
374.		*glumiflora* Klotzsch ex Benth.	Insect	Ovoid-Obovoid
376.		*diosmifolia* Salisb.	Insect	Open-mouthed
379.	Lampro-tis	*dianthifolia* Salisb.	Insect	Ampullaceous
380.		*borboniifolia* Salisb.	Insect	Ampullaceous
381.		*lutea* Berg.	Insect	Ampullaceous
382.		*tenuifolia* L.	Insect	Ampullaceous
383.		*alfredii* Guth. & Bol.	Insect	Ampullaceous
384.		*bracteolaris* Lam.	Insect	Ampullaceous
385.		*steinbergiana* Wendl. f. ex Klotzsch	Insect	Ovoid-Obovoid
386.		*taxifolia* Ait.	Insect	Ampullaceous
387.		*pycnantha* Benth.	Insect	Ovoid-Obovoid
388.		*chlamydiflora* Salisb.	Insect	Ampullaceous
389.		*gnaphaloides* L.	Insect	Ampullaceous
390.		*articularis* L.	Insect	Globose
390.a		*loganii* Compton	Insect	Globose
391.		*caledonica* Spreng.f.	Insect	Ampullaceous
392.		*chlorosepala* Benth.	Insect	Ampullaceous
393.		*laevigata* Bartl.	Insect	Globose
394.		*corifolia* L.	Insect	Globose
394.c		*erasmia* Dulfer	Insect	Ovoid-Obovoid
394.d		*leptantha* Dulfer	Insect	Globose
395.		*rhopalantha* Dulfer	Insect	Globose
396.		*palliiflora* Salisb.	Insect	Globose
397.		*nigrimontana* Guth. & Bol.	Insect	Ovoid-Obovoid
398.		*melanacme* Guth. & Bol.	Insect	Globose
+		*vogelpoelii* H.A. Bak.	Insect	Ovoid-Obovoid
399.	Eury-stegia	*lanuginosa* Andr.	Insect	Ovoid-Obovoid
400.		*bodkinii* Guth. & Bol.	Insect	Globose
401.		*halicacaba* L.	Insect	Ovoid-Obovoid
402.		*monsoniana* L.f.	Insect	Ovoid-Obovoid
403.		*eugenea* Dulfer	Insect	Ampullaceous
404.		*glauca* Andr.	Insect	Ampullaceous
405.		*lanipes* Guth. & Bol.	Insect	Open-mouthed
405.a		*goatcheriana* L. Bol.	Insect	Ovoid-Obovoid
407.		*holosericea* Salisb.	Insect	Open-mouthed
408.		*grisbrookii* Guth. & Bol.	Insect	Globose
408.a		*excavata* L. Bol.	Insect	Globose
+		*occulta* E.G.H. Oliver	Insect	Ovoid-Obovoid

Appendix 1 continued

	Section	Species	Pollination	Corolla shape
+		*calcareophila* E.G.H. Oliver	Insect	Globose
410.	Trigemma	*plumigera* Bartl.	Insect	Ovoid-Obovoid
413.		*tegulifolia* Salisb.	Insect	Globose
414.		*gigantea* Klotzsch ex Benth.	Insect	Open-mouthed
415.		*baccans* L.	Insect	Ovoid-Obovoid
415.a		*sociorum* L. Bol.	Insect	Ovoid-Obovoid
416.		*irregularis* Benth.	Insect	Ovoid-Obovoid
416.a		*stokoei* L. Bol.	Insect	Open-mouthed
418.		*propinqua* Guth. & Bol.	Insect	Open-mouthed
419.		*leucodesmia* Benth.	Insect	Open-mouthed
420.		*triflora* L.	Insect	Open-mouthed
421.		*depressa* L.	Insect	Open-mouthed
422.		*petiolaris* Lam.	Insect	Open-mouthed
423.		*selaginifolia* Salisb.	Insect	Open-mouthed
424.		*gracileps* Guth. & Bol.	Insect	Open-mouthed
425.		*acuta* Andr.	Insect	Open-mouthed
426.		*brevifolia* Soland.	Insect	Open-mouthed
427.		*fimbriata* Andr.	Insect	Open-mouthed
428.		*lycopodiastrum* Lam.	Insect	Ovoid-Obovoid
+		*altevivens* H.A. Bak.	Insect	Ovoid-Obovoid
+		*keerombergensis* H.A. Bak.	Insect	Ovoid-Obovoid
432.		*leucanthera* L.f.	Insect	Open-mouthed
433.		*stenantha* Klotzsch ex Benth.	Insect	Open-mouthed
434.		*consobrina* Guth. & Bol.	Insect	Open-mouthed
435.		*nemorosa* Klotzsch ex Benth.	Insect	Open-mouthed
438.		*peltata* Andr.	Wind	Open-mouthed
439.		*macrotrema* Guth. & Bol.	Insect	Open-mouthed
439.a		*longistyla* L. Bol.	Wind	Open-mouthed
+		*jacksoniana* H.A. Bak.	Insect	Ovoid-Obovoid

Appendix 1 continued

	Section	Species	Pollination	Corolla shape
441.	Eurystoma	*argentea* Klotzsch ex Benth.	Insect	Open-mouthed
442.		*brevicaulis* Guth. & Bol.	Insect	Open-mouthed
443.		*nivea* Sincl.	Insect	Open-mouthed
444.		*lachneifolia* Salisb.	Insect	Open-mouthed
445.		*calycina* L.	Insect	Open-mouthed
445.a		*pseudocalycina* Compton	Insect	Open-mouthed
446.		*comata* Guth. & Bol.	Insect	Open-mouthed
447.		*saxicola* Guth. & Bol.	Insect	Open-mouthed
447.a		*truncata* L. Bol.	Insect	Open-mouthed
448.		*floccifera* Zahlbr.	Insect	Open-mouthed
449.		*lucida* Salisb.	Insect	Open-mouthed
449.a		*adnata* L. Bol.	Insect	Open-mouthed
450.		*mucronata* Andr.	Insect	Open-mouthed
+		*galgebergensis* H.A. Bak.	Insect	Open-mouthed
+		*uysii* H.A. Bak.	Insect	Ovoid-Obovoid
451.	Melastemon	*seriphiifolia* Salisb.	Insect	Open-mouthed
452.		*cubica* L.	Insect	Open-mouthed
453.		*tetrathecoides* Benth.	Insect	Open-mouthed
454.		*humifusa* Hibbert ex Salisb.	Insect	Open-mouthed
455.		*cristiflora* Salisb.	Insect	Open-mouthed
455.a		*lowryensis* L. Bol.	Insect	Open-mouthed
457.		*lavandulifolia* Salisb.	Insect	Open-mouthed
459.		*nervata* Guth. & Bol.	Insect	Open-mouthed
460.a		*granulatifolia* H.A. Bak.	Insect	Open-mouthed
460.b		*pillarkopensis* H.A. Bak.	Insect	Open-mouthed
462.	Gamochlamys	*melanthera* L.	Insect	Open-mouthed
466.a		*blancheana* L. Bol.	Insect	Open-mouthed
467.	Cyatholoma	*thunbergii* Montin	Insect	Globose
468.		*corydalis* Salisb.	Insect	Globose

*Long-proboscid fly (LPF) pollinated species (rhinomyiophilous)