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# THE LONG-PROBOSCID FLY POLLINATION SYSTEM IN SOUTHERN AFRICA<sup>1</sup>

Peter Goldblatt<sup>2</sup> and John C. Manning<sup>3</sup>

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## ABSTRACT

Some 14 species of long-proboscid flies (Diptera) in two families, Nemestrinidae and Tabanidae, with elongated mouth parts are known to pollinate species in several plant families, most importantly Geraniaceae, Iridaceae, and Orchidaceae, across southern Africa. Long-proboscid fly pollination appears to comprise three discrete guilds of flies in the genera *Prosoeca*, *Moegistorhynchus*, and *Stenobasipteron* (Nemestrinidae) and *Philoliche* (Tabanidae). Flies in the three guilds are on the wing at different times of the year and pollinate different suites of plant species, sometimes with different floral characteristics. The three pollinator guilds operate for the most part in different parts of the subcontinent. Where there is geographical overlap, the periods of activity differ. Plants pollinated by long-proboscid flies have flowers with an elongate, cylindrical floral tube, mostly 35–60 cm long, a perianth of specific colors and marking, a floral reward of nectar, and lack floral fragrance. Pollen is not eaten by these flies, and anthers and pollen are often cryptically colored. Flowers are usually zygomorphic and bilabiate, and the petal or tepal lobes have characteristically shaped nectar guides. With few exceptions, the flowers offer ample nectar of sugar concentration mainly in the 20–30% range. Several orchids and one *Pelargonium* using long-proboscid flies for pollination offer no nectar, and pollination is accomplished through floral mimicry and deception. In long-proboscid fly pollination systems, placement of pollen on the insect's body is highly specific, and there are at least six mutually exclusive sites of pollen deposition on an insect's body. When two or more long-proboscid-fly-pollinated plant species co-occur, each typically utilizes a different pollen deposition site. This suggests that pollen contamination is detrimental to reproductive success and that differential pollen deposition sites are important for plants pollinated by long-proboscid flies. Since these flies are the sole or main pollinators of at least 120 plant species and the inferred pollinators of at least 80 more species in southern Africa, they must be considered keystone species in the ecosystems where they occur.

*Key words:* co-evolution, floral ecology, long-proboscid flies, pollination.

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A close association between the form and color of flowers and pollination by a particular pollinator is well known. Convergence in floral morphology among species that rely on the same pollinator class led to the recognition of floral syndromes (e.g., Vogel, 1954; Faegri & van der Pijl, 1979). Moreover, species with morphologically similar flowers that share the same pollinator species constitute a particular pollination guild, an extension of the term describing a group of species that exploit the same class of resources in a similar way (Root, 1967). Likewise, insect species using a particular group of plants as a food resource in a similar way may also be regarded as a guild. A guild is thus a functional unit independent of taxonomic considerations, as are floral syndromes. Although a number of pollination syndromes have been identified in the southern African flora (Vogel, 1954), relatively few guilds have been described. The most striking of those that have been documented is the association be-

tween the satyrid butterfly, *Aeropetes (Meneris) tubbaghia*, and late-summer-flowering species with large, bright red blossoms (Johnson & Bond, 1994). Others include the association of several plant species with magenta to violet-colored flowers and the fly *Prosoeca peringueyi* (Manning & Goldblatt, 1996), the suite of plant species with cream to pale pink flowers blooming in autumn that depend on *P. langipennis* for their pollination (Manning & Goldblatt, 1995), and the *Moegistorhynchus longirostris* guild of the west coast of South Africa.

Pollination by long-proboscid flies is a relatively unusual phenomenon, first recorded in southern Africa by Marloth (1908) and later described in somewhat more detail by Vogel (1954). In their review of insect pollination in the Cape Flora of South Africa, Whitehead et al. (1987) were the first to really recognize long-proboscid fly pollination as a unique pollination system, although very little was then known about either the flies or what plant species

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they pollinated. Thus, long-proboscid fly pollination has only been regarded as a class of pollination system comparable with that of the major pollinator groups or syndromes, bird, bat, bee, butterfly, and muscid/carrion fly, since the late 1980s. Muscid/carrion fly pollination, also called myophily, is classically associated with actinomorphic, bowl- or salver-shaped flowers of pale or dull colors, readily accessible nectar, and well exposed sex organs (Faegri & van der Pijl, 1979). Pollination by Diptera is, in fact, diverse and cannot be usefully regarded as a single pollination syndrome. Sapro-myophily is already distinguished from general myophily because the flies in the syndrome have lapping mouth parts, are attracted by unpleasant odors of decay or fermentation, and are associated with flowers with dull colors, often with mottled pigmentation, and hairy or frilled petals or tepals. Long-proboscid fly pollination (or rhinomyophily, viz. Rebelo et al., 1985) may readily be distinguished from classical myophily and its specialized derivative, sapromyophily, and differs in all criteria enumerated by Faegri and van der Pijl for this myophily. Long-proboscid fly flowers are typically zygomorphic, normally have an elongate floral tube, and have bright coloration. The sex organs are presented in a wide range of orientations, sometimes concealed within or above the mouth of the tube, or are elongate and held distant from the source of the nectar reward in a unilateral, arcuate (adaxial) or declinate (abaxial) disposition.

Although pollination by long-proboscid flies has been described from various parts of the world, the system as we define it here is restricted to the Himalayan Region (Fletcher & Son, 1931; Dierl, 1968) and southern Africa, where the system has received a fair amount of attention since 1990 (e.g., Goldblatt et al., 1995; Manning & Goldblatt, 1996, 1997; Johnson & Steiner, 1995, 1997). So-called long-proboscid fly pollination described in the literature, for example, by Grant and Grant (1965) in California, refers to bombyliid flies with probosces less than 15 mm long and differs from the pollination system we regard as long-proboscid fly pollination. Here we review long-proboscid fly pollination, report additional examples of pollination by long-proboscid flies, and assess the importance of the system in the southern African flora relative to other pollination systems.

## REVIEW OF LONG-PROBOSCID FLY POLLINATION

### LONG-PROBOSCID FLIES

*Definition and morphological characteristics.* We define long-proboscid flies here as those

insects that have mouth parts at least 15 mm long and a body length of more than 15 mm. Fifteen species in two families, Nemestrinidae and Tabanidae, are known to have mouth parts this long, 14 of them restricted to the southern African region, Lesotho, Namibia, South Africa, and Swaziland (Fig. 1, Table 1), and one to the Himalayas (Dierl, 1968). Adult morphs of these flies depend largely or exclusively on floral nectar for their nutrition and are avid foragers of nectar-rich flowers (female Tabanidae also require a blood meal). Their visits to the flowers of some plants result in the passive accumulation of pollen or pollinaria as they brush against anthers, and in turn, the passive transference of pollen or pollinaria to stigmas during visits to other flowers of the same species. Most other Nemestrinidae and Tabanidae have substantially shorter mouth parts and, although they also feed on nectar and pollinate plants, they are not known to be the only pollinator(s) of any plants. Instead they share pollen resources with other insect taxa including long-tongued bees, Lepidoptera, hopline beetles, and bee flies (Bombyliidae) (Goldblatt et al., 1995, 1998b, in prep.). The tabanid, *Philoliche aethiopica*, and the acrocerid flies, *Psilodera* spp. (Goldblatt et al., 1997; Potgieter et al., 1999), have mouthparts of intermediate length, mostly 12–15 mm long, and they are provisionally excluded from consideration here: their shorter mouthparts prevent them from foraging effectively on flowers of plant species that have exclusively long-proboscid fly pollinators.

Long-proboscid flies are large-bodied insects, typically measuring 15–24 mm from the tip of the abdomen to the base of the proboscis. Mouth parts are as long as, or often substantially longer than, the insect's body, the most extreme example being *Moegistorhynchus longirostris*—individuals along the Cape west coast have been recorded with probosces up to 100 mm long (Fig. 2). Foraging behavior is similar in all species, irrespective of family or genus, and although flies have been described as hovering while foraging (Struck, 1997), this is not the usual pattern. Our observations show that flies firmly grasp tepal or petal lobes or other floral organs as they forage for nectar and while doing so they continue to vibrate their wings rapidly (Goldblatt et al., 1995; Goldblatt & Manning, 1999) (Fig. 3A–D).

Foraging patterns vary, but our observations show that long-proboscid flies are seldom flower constant. While flies sometimes forage for a time on a particular floral form and may visit a particular species more frequently than any other, more often their foraging appears to be random, and foraging

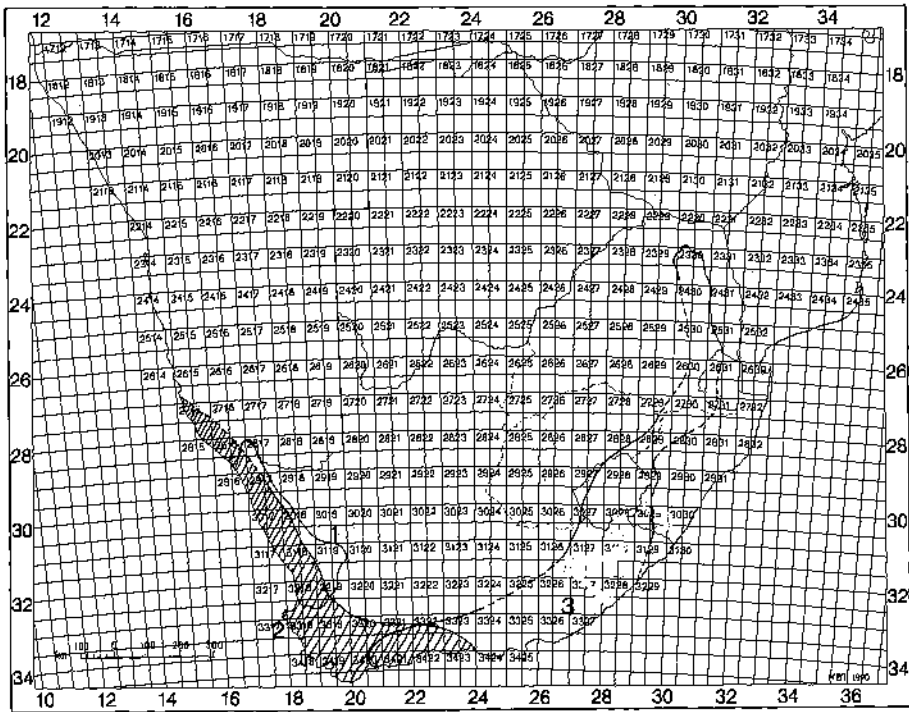


Figure 1. Southern Africa, showing the geographical extent of each of the three long-proboscid fly pollination guilds. —1. The *Prosoeca peringueyi* guild. —2. The *Moegistorhynchus-Philoliche* guild (shaded). —3. The *Prosoeca ganglbaueri* guild. The ranges of guilds 1 and 2 correspond almost exactly to the southern African winter-rainfall zone. Note the limited geographic overlap that does not coincide temporally.

bouts may include flowers of several different species, some of which even have different shapes, sizes, and colors. This emphasizes that long-proboscid flies can and do forage on a wide range of flowers. Long-tubed flowers, however, are the only ones that offer a secure reward, and because of their size, a significantly larger reward, and one that is not available to most other nectarivorous insects.

**Zoogeography.** The southern African long-proboscid flies have variable geographic ranges (Table 1). All but one of the species are, however, restricted to one or the other of the two major climatic and biotic zones of southern Africa, the winter-rainfall zone in the southwest, and the summer-rainfall zone, which covers the rest of the subcontinent (Fig. 1). *Prosoeca ganglbaueri* has the widest range and extends from the Northern Province of South Africa through eastern southern Africa to the Kleinswartzberg in the south (at the interior edge of the winter-rainfall zone), a distance of over 1500 km. In contrast, and despite pollination research in the area, *P. rubicunda* is known from one specimen from the southwestern Cape, while *P. nitidula* is restricted to the Cape Peninsula at the extreme southwestern

edge of the subcontinent and the center of the winter-rainfall zone. Evidently also rare, *Moegistorhynchus* sp. is known from two high-mountain sites in the southwestern Cape.

#### PLANT SPECIES

Plants that depend on long-proboscid flies for their pollination comprise a varied group taxonomically and morphologically (Table 2). They range from seasonal perennials, mostly geophytes with corms, bulbs, or tubers (Amaryllidaceae, Iridaceae, Orchidaceae, some Geraniaceae), to shrubs (Ericaceae, some Geraniaceae, Lamiaceae, Scrophulariaceae). No annuals or trees have so far been found with this pollination system.

**Floral characteristics.** Flowers of most species have in common a long floral tube (Figs. 4, 5) (we use the term here to include a corolla or perianth tube, tepal spurs of orchids, as well as the receptacular tube of *Pelargonium*), usually exceeding 20 mm, and usually produce ample nectar. Notable exceptions are *Aristea spiralis* (Iridaceae) and species of *Brunsvigia* and *Nerine* (Amaryllidaceae), which

Table 1. Proboscis length, peak months of activity, and geographic ranges of long-proboscis flies in southern Africa. Data are taken from our observations, the literature, and museum collections. So little is known about *Prosoeca rubicunda* that its inclusion in the *Moegistorhynchus-Philoliche* guild is tentative. Taxonomic affiliation: Nemestrinidae—*Moegistorhynchus*, *Prosoeca*, *Stenobasipteron*; Tabanidae—*Philoliche*. WRZ = winter-rainfall zone, SRZ = summer-rainfall zone. \*Note that we regard *M. braunsii* and *M. perplexus* (each known only from their type collections) as synonyms of *M. longirostris*.

Fly species	Proboscis length range mm (N)	Months on the wing	Geographic range
<i>Prosoeca peringueyi</i> guild			
<i>P. peringueyi</i>	(15-)25-40 (15)	July-Sep.	WRZ: S Namibia to N Western Cape
<i>P. sp. nov.</i>	32-43 (8)	Aug.-Sep.	WRZ: Northern Cape (Calvinia District)
<i>Moegistorhynchus-Philoliche</i> guild			
<i>M. longirostris</i> *	(35-)42-80 (14)	Sep.-Nov.	WRZ: Western and Northern Cape coast and interior
<i>M. sp. nov.</i>	ca. 21 (1)	Jan.	WRZ: Western Cape
<i>Philoliche gulosa</i>	18-33 (9)	Sep.-Nov.	WRZ: Western Cape, mainly interior
<i>P. rostrata</i>	21-27 (7)	Oct.-Nov.	WRZ: Western Cape, coast and interior
<i>Prosoeca nitidula</i>	18-28 (5)	Oct.-Jan.	WRZ: Western Cape (only Cape Peninsula)
<i>P. rubicunda</i>	ca. 21 (1)	Jan.	WRZ: Western Cape (only Caledon District)
<i>Prosoeca ganglbaueri</i> guild			
<i>P. ganglbaueri</i>	(17-)25-42 (12)	Jan.-Apr.	SRZ & WRZ: Northern Province to E Western Cape incl. Lesotho
<i>P. longipennis</i>	38-40 (3)	Mar.-Apr.	WRZ: Southern Cape
<i>P. robusta</i>	20-46 (7)	Feb.-Apr.	SRZ: Mpumalanga
<i>Stenobasipteron wiedmannii</i>	18-30 (5)	Feb.-Apr.	SRZ: Mpumalanga and KwaZulu-Natal

have floral tubes less than 10 mm long. Species with short floral tubes have elongate stamens so that the body of a foraging fly will brush against anthers even when its proboscis much exceeds the length of the tube.

Flower colors fall into two major groups (Goldblatt et al., 1995; Manning & Goldblatt, 1996, 1997). In northern Western Cape Province and Namaqualand flowers are typically intensely dark red to purple or violet with pale nectar guides (Fig. 4). In the rest of southern Africa, however, these colors are rarely associated with long-proboscis fly flowers. Instead, flowers are usually shades of cream to pink, with pink to red nectar guides (Fig. 5). A few species may have pale blue or mauve flowers, but species of *Nivenia* (Iridaceae) are exceptional in having deep blue perianths. Again with few exceptions, the nectar guides consist of longitudinal streaks. Flower form is usually zygomorphic and bilabiate with unilateral, arcuate stamens and style (Figs. 4G-L, 5F, G) or with declinate stamens and style (Figs. 4D-F, 5B-E). A few species of *Erica*, *Hesperantha*, *Ixia*, *Nivenia*, *Romulea*, and one of *Lapeirousia* have actinomorphic flowers (Figs. 4A-C, 5A).

Anthers and pollen are often unconventionally pigmented and frequently match the color of the

perianth, or are simply a dull blue-gray to mauve (Goldblatt et al., 1995). Some *Gladiolus* and *Tritonia* species with cream flowers, however, have dark purple pollen (Goldblatt & Manning, 1999). It has been suggested that unusually colored pollen is an example of crypsis, making the pollen less conspicuous to pollen-collecting insects (Manning & Goldblatt, 1996). In *Pelargonium* species, anthers and pollen are bright red to orange and may contribute to the floral signal to flies (Goldblatt et al., 1995), especially if the petals are weakly marked.

Scent production is rare (Table 2). In the Iridaceae only *Babiana sambucina* has strongly scented flowers, while *B. framesii* often has lightly fragrant flowers. In the Amaryllidaceae, species of *Brunsvigia* typically have a light sweet fragrance.

A particularly notable aspect of long-proboscis fly pollinated plants is the range of stamen orientation and length, which are directly related to the site of deposition of pollen on the body of a fly. Actinomorphic flowers have symmetrically disposed stamens either held close to the mouth of the floral tube, or in *Erica*, within the tube. In *Aristea spiralis* the anthers are held 16-20 mm from the vestigial floral tube. *Nivenia* species either have the anthers held at least 10 mm from the mouth of the tube, or in the distylous *N. argentea* and *N. steno-*

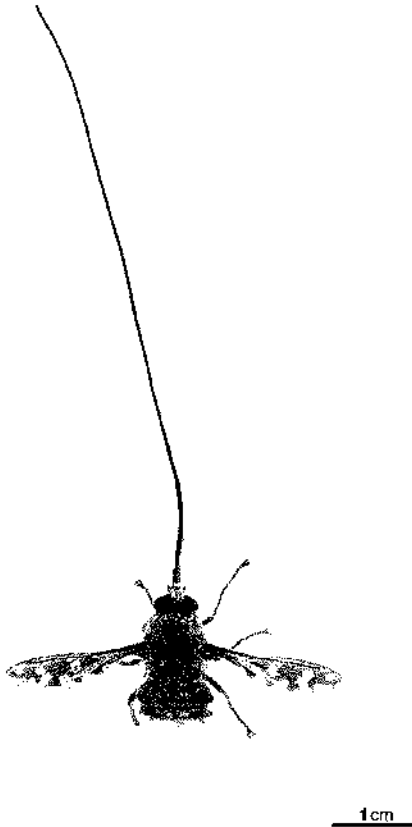


Figure 2. *Moegistorhynchus longirostris*, the fly with the longest proboscis of all southern African long-proboscid flies. The tongue measures between 35 and 100 mm long. Note the scattering of pollen over the dorsal part of the fly's body.

siphon stamens of the pin (long-styled and short-stamened) morph are held just above the apex of the floral tube. In zygomorphic flowers, the stamens are unilateral and either arcuate (arching above the mouth of the tube), as in most Iridaceae, or declinate (arching below the mouth of the tube), as in *Pelargonium* (Fig. 4D–F), *Geissorhiza* (Fig. 5B), and the amaryllids *Brunsvigia* and *Nerine*. In the latter two genera, the filaments are extended forward for 35–40 mm, so that the anthers are held at least this distance from the nectar source. Stamen length is notably variable in *Pelargonium*, species of which have anthers held close to, or up to, 15 mm from the mouth of the floral tube. Pollen deposition on foraging flies is dorsal in species with arcuate stamens and ventral in species with declinate stamens. When anthers are held close to the mouth of the

floral tube, pollen deposition is on the frons and/or the base of the proboscis.

#### COMPARATIVE POLLINATION ECOLOGY OF THE THREE GUILDS

##### SUBDIVISION OF THE LONG-PROBOSCID FLY POLLINATION SYNDROME

We propose recognizing three separate pollination guilds or systems within the long-proboscid fly pollination strategy. The flies that belong to each system show little or no overlap with those of other systems in plants visited or season on the wing, although there is some overlap in geographic range (Fig. 1). Within each system there are well-defined guilds of plant species that have one or occasionally two fly species as their sole pollinator. A few plant species may be pollinated by different fly species in different parts of their ranges. Thus, *Lapeirousia silenoides* is pollinated only by *Prosoeca peringueyi*, but *L. jacquinii* may be pollinated by *P. peringueyi* or, on the Bokkeveld Plateau, by *Prosoeca* sp. nov. Likewise, *L. fabricii* has been recorded as pollinated by *Moegistorhynchus longirostris* at some sites, by *Philoliche gulosa* at others, and by both flies at one site (Manning & Goldblatt, 1997). The occasional presence of two long-proboscid fly species at a few sites has also been documented by Goldblatt and Manning (1999) both in Western Cape and Mpumalanga Provinces, but this appears to be a relatively infrequent situation.

1. The *Prosoeca peringueyi* guild includes two fly species, *P. peringueyi* and *Prosoeca* sp. nov. (Table 1). With complementary ranges in southern Namibia and Namaqualand to the Olifants River Valley and the Western Karoo in South Africa (Fig. 1), these two flies are active from July to late September. The range is thus restricted to the western half of the southern African winter-rainfall zone and activity to the cooler months of the year. The two flies pollinate separate suites of species with similar floral presentation, but at least the widespread *Babiana framesii*, two varieties of *B. sambucina*, and *Lapeirousia jacquinii* share both flies as their sole pollinators (Goldblatt et al., 1995; Manning & Goldblatt, 1996).

Plants in the guild (Table 2) stand out in having flowers intensely pigmented in shades of magenta, deep purple, or violet, the lower, or all the petal or tepal lobes in the case of actinomorphic flowers, with cream to yellow markings and areas of darker pigmentation (Fig. 4). Tepal lobes are often relatively small, 12–15 mm long (e.g., *Lapeirousia jacquinii*, *L. silenoides*, *Romulea hantamensis*), but some species of *Babiana* belonging to the guild

have relatively large flowers with tepal lobes up to 28 mm long. Anthers and pollen are often shades of mauve to violet or cream.

The floral tube in most species of the *Prosoeca peringueyi* guild is at least 20 mm long, and usually in the 30–45 mm range. All members of the guild flower in the late winter to late spring, late July to mid September, and are geographically restricted to the southern African west coast and near interior (Namaqualand and the northwestern Cape, South Africa, and southwestern Namibia). Some plant species in the guild have somewhat wider ranges than their pollinators and today reproduce sexually only by autogamously produced seed in the parts of their ranges where no pollinating flies occur (e.g., *Lapeirousia jacquinii*, *Sparaxis metelerkampiae*) (Manning & Goldblatt, 1996; Goldblatt et al., in prep.).

2. The *Moegistorhynchus-Philoliche* guild, named for the most conspicuous fly genera in the system, includes six or seven fly species. The two tabanids, *P. rostrata* and *P. gulosa*, have the widest ranges, collectively extending from southern Namibia to the southeastern Cape (Fig. 1). The three *Moegistorhynchus* species and the one or two *Prosoeca* species of the system have narrower ranges in the southwestern Cape (Table 1). Flies of this system are mostly active from late spring to early summer, mid September to November, but are still on the wing until January locally at higher elevations. Species pollinated by this group of flies mostly have a similar floral presentation, and the particular pollinator depends on geography. The same species may be pollinated by up to three different flies over its entire range. Although the geographical ranges of the *Pr. peringueyi* and *Moegistorhynchus-Philoliche* systems overlap in western southern Africa, they overlap very little in period of activity of fly species and, as far as is known, not at all in plants pollinated.

Plants in the *Moegistorhynchus-Philoliche* guild mostly have flowers in shades of white to cream, usually with pink undertones, or pale to deep pink (Fig. 5). Nectar guides are deep pink or red, occasionally with a white streak in the center of each dark mark. On the southern African west coast, flowers often have relatively large tepal lobes, 30–50 mm long (e.g., *Gladiolus angustus*, *G. undulatus*, *Pelargonium longicaule*), but *Babiana tubulosa*, *Lapeirousia anceps*, and *P. appendiculatum* have fairly small, inconspicuous tepal or petal lobes, up to 15 mm long. The longest floral tubes (60–110 mm long) are found in west coast populations of *G. angustus*, *L. anceps*, and *P. appendiculatum*, and these species are associated exclusively with a sin-

gle pollinator, *Moegistorhynchus longirostris*. There, this fly has a proboscis at least 65 mm long, whereas in central Namaqualand, to the north, it has a proboscis only 37–45 mm long. Populations of *G. angustus* and *L. anceps* elsewhere have shorter tubes and are pollinated by *Philoliche* species, which have correspondingly shorter probosces.

Several plant species from the Roggeveld and Hantam areas of the western Karoo including *Babiana spathacea*, *Disa karooica*, and *Romulea syringodeoflora* (white-flowered race), as well as several species of *Pelargonium*, all of which have cream to white flowers with red markings and elongate floral tubes, present a problem in the context of long-proboscis fly pollination. Although they bloom from October to early December, when *Philoliche gulosa* and *P. rostrata* are on the wing, and have flowers that appear to be adapted for pollination by long-proboscis flies, no long-proboscis species have been captured or recorded in this area. Can the legitimate pollinator(s), whether one of these *Philoliche* species or another fly species, be extinct locally, as suggested by S. D. Johnson (pers. comm.)?

Too little is known about the Western Cape species, *Prosoeca rubicunda*, to confidently place it in one of the long-proboscis fly guilds, but its apparent period of activity, January, suggests that it may be a local extension of the *Moegistorhynchus-Philoliche* guild, which is centered in Western Cape Province. Several plant species from the Caledon-Bredasdorp area of the winter-rainfall zone that flower in the summer, from November to January, including *Nivenia concinna*, *N. stokoei*, and *Tritoniopsis flexuosa* (Iridaceae) and *Pelargonium caucalifolium* (Geraniaceae), have no known pollinator although they have flowers that conform closely to the long-proboscis fly type.

3. The *Prosoeca ganglbaueri* guild, named for the most widespread and common fly species in the system, operates in the southern summer and autumn, from January to April, and largely in eastern southern Africa in areas of summer precipitation (Fig. 1), but also in the eastern half of the winter-rainfall zone that receives appreciable summer precipitation. As treated here, the *P. ganglbaueri* guild includes four fly species (Table 1). While *P. ganglbaueri* extends from Northern Province southward to the Kleinswartberg Mountains in Western Cape Province, *P. longipennis* is restricted to the southern Cape coastal belt. Because of the opposed seasonality there is virtually no overlap in plant species with the *P. peringueyi* and *Moegistorhynchus-Philoliche* systems. The ranges of the flies *Prosoeca longipennis* and *P. ganglbaueri*, in the south of its

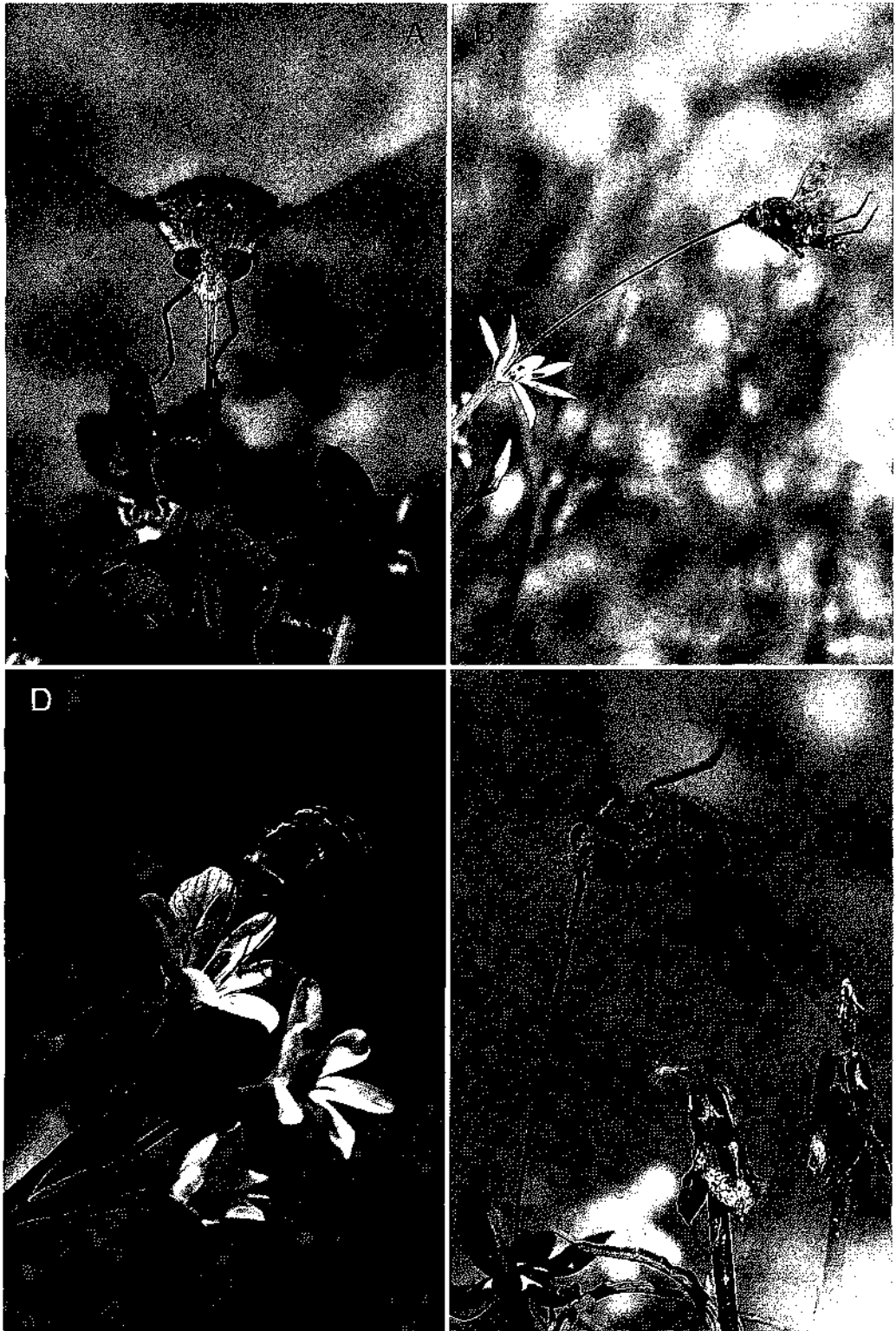


Figure 3. Long-proboscid flies foraging on their flowers. —A. *Prosoeca peringueyi* hovering above a cluster of *Lapeirousia silenoides* flowers. —B. *Moegistorhynchus longirostris* about to forage on a flower of *Lapeirousia anceps*.



range, overlap the eastern half of the range of flies belonging to the *Moegistorhynchus-Philoliche* guild, but the months of activity of the flies in the two systems differ.

Guilds of plant species pollinated by *Prosoeca ganglbaueri*, *P. longipennis*, and *P. robusta* overlap to some extent. For example, populations of *Tritoniopsis revoluta* occur within the ranges of *P. ganglbaueri* and *P. longipennis*; *Disa amoena* pollinaria have been found on both *P. ganglbaueri* and *P. robusta*, and both flies have been captured while foraging on *Gladiolus calcaratus* and *Watsonia wilmsii*. Likewise, *P. ganglbaueri* and *P. longipennis* have been observed and captured pollinating *Pelargonium dipetalum* in different parts of its range. No overlap has so far been encountered in the species pollinated by *Stenobasipteron wiedmannii*, and further investigation may show this fly represents a guild separate from the *P. ganglbaueri* guild of flies.

Flowers pollinated by flies in the *Prosoeca ganglbaueri* guild are usually pink with dark pink to red markings, but *Zaluzianskya microsiphon* has cream petals, pink on the reverse, and *Gladiolus calcaratus* has white flowers. *Nivenia stenosisiphon* is unusual in having actinomorphic, uniformly deep blue flowers, at least to the human eye. Thus, in general flowers pollinated by flies of the *P. ganglbaueri* guild resemble those pollinated by flies of the *Moegistorhynchus-Philoliche* guild. Species pollinated by *P. longipennis*, a fly restricted to the southern Cape coastal belt, have flowers with relatively small petal or tepal lobes, mostly ca. 10 mm long, and a corolla or perianth that ranges from cream to pale pink or salmon, usually with darker pink or red on the lower (*Gladiolus*, *Tritoniopsis*), or upper (*Pelargonium*), or all the lobes (*Cyrtanthus leptosiphon*) (Manning & Goldblatt, 1995). Flowers pollinated by *Stenobasipteron wiedmannii* are shades of pale blue, mauve, or pink (Goldblatt & Manning, 1999; Potgieter et al., 1999) and usually have small tepal or petal lobes, but species pollinated by *P. ganglbaueri* and *P. robusta* often have large lobes.

#### FLORAL REWARD—NECTAR

*Nectar volume.* Nectar production is usually ample, and quantities mostly range from 1.1 to 5  $\mu$ l per flower in a standing crop (unbagged flowers)

(Table 3). Large-flowered species like *Gladiolus angustus* and *G. undulatus* may produce up to 10  $\mu$ l of nectar per bloom. *Aristea spiralis* is unusual in having flowers that offer less than 0.5  $\mu$ l of nectar. *Disa draconis*, *D. harveiana*, and *D. oreophila*, *Pelargonium sericifolium*, and *Hesperantha scopulosa* produce no nectar (Table 3) and evidently depend for their pollination on deceit, their flowers closely resembling those of other members of their respective pollination guilds (Goldblatt et al., 1995; Johnson & Steiner, 1995, 1997; Manning & Goldblatt, 1997).

*Nectar sugar chemistry.* In species of the Iridaceae, Lamiaceae, and Orchidaceae, nectar is sucrose-rich to sucrose-dominant (ratio of sucrose to hexose sugars greater than 1—see Table 3), but nectar in most species of *Pelargonium* examined is hexose-rich or hexose-dominant. Nectar sugar concentrations are mostly in the 20–30% sucrose equivalent range, but may be as low as 19% (*Romulea hantamensis*) or as high as 33% (*P. incrassatum*) (Table 3). Two species of *Hesperantha*, *H. grandiflora* and *H. galpinii*, also produce nectar of unusually low sugar concentration, less than 18% sucrose equivalents.

#### POLLEN PLACEMENT

Pollen placement on the body of a fly appears to be an important consideration in long-proboscis fly pollination systems. At all sites that we have investigated, the number of plant species utilizing a particular long-proboscis fly for their pollination appears to be closely correlated with the number of pollen deposition sites (Manning & Goldblatt, 1996, 1997). Typically the frons and base of the proboscis, the dorsal part of the head and thorax, and the ventral part of the thorax and abdomen are used by different plant species for pollen deposition (Fig. 6). In the case of some Orchidaceae, pollinaria are usually deposited near the base of the proboscis (Johnson & Steiner, 1995, 1997). The need for specific sites for pollen or pollinarium deposition is presumably related to the behavior of long-proboscis flies, which are not flower constant. Instead, they visit flowers of different species in an apparently random pattern on foraging bouts (Goldblatt et al., 1995; Goldblatt & Manning, 1999). The deposition of more than one pollen species at the

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—C. *Prosoeca* sp. nov. about to insert its proboscis into the long perianth tube of *Lapeirousia oreogena*. —D. *Philoliche rostrata* about to forage on *Tritonia flabellifolia*; note the heavy deposit of purple *Tritonia* pollen on the dorsal part of the thorax.

Table 2. Floral characters of plants pollinated by long-tongued flies arranged by guild. Abbreviations: b = blue with light throat; cr = pale cream with red markings; p = pale pink or deep pink with red or purple nectar guides; v = vivid (red, purple, or violet shades with contrasting pale nectar guides); wh = white. Scent indicated by - = absent; + = present; ++ = present and strong. For tube length we give only the functional length, not total length—in *B. curviscapa*, *B. dregei*, and *B. framesii*, all acaulescent species, the lower part of the tube is closed and only serves to raise the flower above the foliage. Additional species inferred on the basis of floral presentation to belong to particular guilds, but with no insect visits recorded, are listed in parentheses. References, column eight, are as follows: 1 = Goldblatt et al. (1995) and Manning & Goldblatt (1996); 2 = Manning & Goldblatt (1997); 3 = Goldblatt & Manning (1999); 4 = Goldblatt et al. (1999); 5 = Johnson & Steiner (1995); 6 = Johnson & Steiner (1997); 7 = Struck (1997); 8 = Manning & Goldblatt (1995); 9 = Vogel (1954); 10 = Goldblatt & Bernhardt (1990); 11 = Potgieter et al. (1999); 12 = Goldblatt & Manning (new data; for methodology see Goldblatt et al. (1998a), Goldblatt & Manning (1999)).

Species	Flower			Pollinator	Mouth part mm	Floral tube mm	Reference
	Symmetry	Color	Scent				
<i>Prosopoca peringueyi</i> pollination system							
Geraniaceae							
<i>Pelargonium</i>							
<i>echinatum</i> Curtis	z	wh	-	<i>Pr. peringueyi</i>	n/a	n/a	7
<i>incrassatum</i> (Andr.) Sims	z	v	-	<i>Pr. peringueyi</i>	28-33	30-40	1
<i>magentum</i> van der Walt	z	v	-	<i>Pr. peringueyi</i>	30-35	33-39	1
<i>sericifolium</i> van der Walt	z	v	-	<i>Pr. peringueyi</i>	35-40	35-60	1
Iridaceae							
<i>Babiana</i>							
<i>curviscapa</i> G. J. Lewis	z	v	-	<i>Pr. peringueyi</i>	25-28	26-36	1, 12
<i>dregei</i> Baker	z	v	-	<i>Pr. peringueyi</i>	25-28	30-35	1
<i>ecklonii</i> Klatt	z	v	-	<i>Pr. peringueyi</i>	27-32	40-50	12
<i>flabellifolia</i> G. J. Lewis	z	v	-	<i>Pr. sp. nov.</i>	40-45	40-65	1
<i>framesii</i> L. Bolus	z	v	+	<i>Pr. sp. nov.</i> and <i>Pr. peringueyi</i>	40-45	45-50	1
<i>geniculata</i> G. J. Lewis	z	v	-	<i>Pr. peringueyi</i>	30-35	35-45	1
<i>pubescens</i> G. J. Lewis	z	v	-	<i>Pr. peringueyi</i>	32-35	44-50	1
<i>sambucina</i>							
var. <i>longibracteata</i> G. J. Lewis	z	v	++	<i>Pr. sp. nov.</i>	40-45	40-50	12
var. <i>unguiculata</i> G. J. Lewis	z	v	+	<i>Pr. peringueyi</i>	40-45	40-50	12
<i>Hesperantha</i>							
<i>latifolia</i> (Klatt) M. P. de Vos	z	v	-	<i>Pr. peringueyi</i>	15-25	20-25	1
<i>Lapeirousia</i>							
<i>dolomitica</i> subsp.							
<i>dolomitica</i> Dinter	z	v	+	<i>Pr. peringueyi</i>	33-35	35-40	1
<i>jacquinii</i> N. E. Br.	z	v	-	<i>Pr. sp. nov.</i> and <i>Pr. peringueyi</i>	33-40	33-35	1
<i>oreogena</i> Schltr.	a	v	-	<i>Pr. sp. nov.</i>	40-45	53-70	1
<i>pyramidalis</i> subsp. <i>regalis</i> Goldblatt & J. C. Manning	z	v	-	<i>Pr. peringueyi</i>	32-34	40-47	1
<i>silenoides</i> (Jacq.) Ker Gawl.	z	v	-	<i>Pr. peringueyi</i>	35-40	43-55	1
<i>violacea</i> Goldblatt	z	v	-	<i>Pr. peringueyi</i>	32-35	34-40	1
<i>Romulea</i>							
<i>hantamensis</i> (Diels) Goldblatt	a	v	-	<i>Pr. sp. nov.</i>	40-45	50-70	1
<i>Sparaxis</i>							
<i>metelerkampiae</i> (L. Bolus) Goldblatt & J. C. Manning	z	v	-	<i>Pr. peringueyi</i>	30-35	40-45	1

Table 2. Continued.

Species	Flower			Pollinator	Mouth part mm	Floral tube mm	Reference
	Symmetry	Color	Scent				
[Inferred members of the guild—Geraniaceae: <i>Pelargonium cortusifolium</i> L'Her., <i>P. crassicaule</i> L'Her. Iridaceae: <i>Lapeirousia dolomitica</i> subsp. <i>lewisiana</i> (B. Nord.) Goldblatt, <i>Geissorhiza kamiesmontana</i> Goldblatt, <i>Hesperantha oligantha</i> Diels, <i>H. purpurea</i> Goldblatt, <i>Romulea kamiesensis</i> M. P. de Vos, <i>Sparaxis roxburghii</i> (Baker) Goldblatt, <i>Tritonia marlothii</i> M. P. de Vos, <i>Xenoscapa uliginosa</i> Goldblatt & J. C. Manning. Scrophulariaceae: <i>Jamesbrittenia fruticosa</i> (Benth.) Hilliard]							
<i>Moegistorhynchus</i> – <i>Philoliche</i> pollination system							
Campanulaceae							
<i>Lobelia</i>							
<i>coronopifolia</i> L. (pink form)	a	p	–	<i>Ph. gulosa</i>	18–20	ca. 20	12
Geraniaceae							
<i>Pelargonium</i>							
<i>articulatum</i> (Cav.) Willd.	z	cr	–	<i>Ph. rostrata</i>	n/a	50–75	7
<i>barklyi</i> Scott Elliot	z	cr	–	<i>Ph. rostrata</i>	n/a	n/a	7
<i>elongatum</i> (Cav.) Salisb. (also as <i>P. zonale</i> )	z	cr	–	<i>Ph. gulosa</i> and <i>Ph. rostrata</i>	22–34 22–31	24–32 24–32	1, 2, 12
<i>laevigatum</i> (L.f.) Willd.	z	p	–	<i>Ph. gulosa</i> and <i>Ph. rostrata</i>	n/a n/a	n/a n/a	7 7
<i>longicaule</i> Jacq.	z	p	–	<i>M. longirostris</i> <i>Ph. rostrata</i>	65–72 ca. 35	40–90 55–66	2 5
<i>myrrhifolium</i> (L.) L'Her.	z	cr	–	<i>Ph. rostrata</i>	23–27	18–23	5
<i>oxyphyllum</i> DC.	z	p	–	<i>Ph. gulosa</i>	18–20	20–25	12
<i>patulum</i> Jacq.	z	p	–	<i>Ph. rostrata</i>	25–27	15–20	2, 7
<i>petitatum</i> (L.) L'Her.	z	p	–	<i>Ph. rostrata</i> and <i>Ph. gulosa</i>	27–31 17–19	22–33 22–33	7, 12 12
<i>praemorsum</i> (Andr.) Dietr.	z	cr	–	<i>M. longirostris</i>	27–40	35–40	2
Iridaceae							
<i>Aristea</i>							
<i>spiralis</i> (L.f.) Ker Gawl.	z	b/w	–	<i>Ph. gulosa</i>	16–18	ca. 1.5	12
<i>Babiana</i>							
<i>tubulosa</i> (Burm. f.) Ker Gawl.	z	w	–	<i>M. longirostris</i>	70–95	65–72	2
<i>Geissorhiza</i>							
<i>bonaspei</i> Goldblatt	z	p	–	<i>Ph. rostrata</i> and <i>Pr. nitidula</i>	22–24 18–24	22–30 22–30	12 12
<i>excapa</i> (Thunb.) Goldblatt	z	p	–	<i>M. longirostris</i>	65–70	65–80	2
<i>confusa</i> Goldblatt	z	p	–	<i>Ph. rostrata</i> and <i>Ph. gulosa</i>	25–27 22–24	35–40 35–40	12 12
<i>Gladiolus</i>							
<i>angustus</i> L.	z	p	–	<i>M. longirostris</i>	67–70	70–110	2
<i>carneus</i> D. Delaroché	z	p	–	<i>Ph. rostrata</i> and/or <i>Pr. nitidula</i>	22–24 18–24	32–37 32–37	3 3
<i>floribundus</i> Jacq.	z	cr	–	<i>Ph. rostrata</i> and <i>Ph. gulosa</i>	30–34 17–18	45–60 45–60	3 3
<i>monticola</i> G. J. Lewis ex Goldblatt & J. C. Manning	z	p	–	<i>Ph. rostrata</i> , <i>Pr. nitidula</i>	25–27 18–20	22–30 22–30	3 3
<i>rhodanthus</i> J. C. Manning & Goldblatt	z	p	–	<i>M. sp. nov.</i>	18–20	23–27	3
<i>undulatus</i> Jacq.	z	cr	–	<i>Ph. rostrata</i>	25–27	52–75	2, 3
<i>vigilans</i> Barnard	z	p	–	<i>Ph. rostrata</i>	23–25	35–40	3
<i>virgatus</i> Goldblatt & J.C. Manning	z	p	–	<i>Ph. rostrata</i>	18–20	23–27	3

Table 2. Continued.

Species	Flower			Pollinator	Mouth part mm	Floral tube mm	Reference
	Sym- metry	Color	Scent				
<i>Ixia</i>							
<i>bellendenii</i> R. C. Foster	a	p	—	<i>Ph. gulosa</i>	18–22	30–32	4
<i>paniculata</i> D. Delaroché	a	cr	~	<i>M. longirostris</i> and <i>Ph. rostrata</i>	67–70 n/a	65–75	2, 6 12
<i>paucifolia</i> G. J. Lewis	a	cr	—	<i>Ph. gulosa</i> and <i>Ph. rostrata</i>	18–22 ca. 16	26–28 16–18	4 4
<i>Lapeirousia</i>							
<i>anceps</i> (L.f.) Ker Gawl.	z	p	~	<i>M. longirostris</i> and <i>Ph. gulosa</i>	52–63 29–34	65–76	1, 2 2
<i>fabricii</i> (D. Delaroché) Ker Gawl.	z	cr/p	—	<i>M. longirostris</i> and <i>Ph. gulosa</i>	42–70 29–34	38–65 n/a	1, 2 2
<i>Tritonia</i>							
<i>crispa</i> (L. f.) Ker Gawl.	z	p	—	<i>M. longirostris</i> and <i>Ph. gulosa</i>	42–46 29–34	40–48	2 2
<i>flabellifolia</i> (D. Delaroché) G. J. Lewis	z	p	—	<i>Ph. rostrata</i> and <i>Ph. gulosa</i>	27–31 17–18	45–55	12 12
<i>pallida</i> Ker Gawl.	z	p	—	<i>Ph. rostrata</i>	30–34	45–55	12
<i>Watsonia</i>							
<i>barbonica</i> (Pourt.) Goldblatt	z	p	+	<i>Ph. rostrata</i> , <i>Pr. nitidula</i> , anthophorine and megachilid bees, <i>Ph. lateralis</i>	19–22 18–19.5	14–18	12 12
<i>paucifolia</i> Goldblatt	z	p	—	<i>M. sp. nov.</i>	18–20	22–30	12
Orchidaceae							
<i>Disa</i>							
<i>draconis</i> (L. f.) Sw.	z	cr	—	<i>M. longirostris</i> , <i>Ph. rostrata</i>	ca. 57 ca. 35	ca. 48	6 6
<i>harveiana</i> Lindl.	z	pb	—	<i>Ph. rostrata</i>	23–27	32–38	6
[Inferred members of the guild—Ericaceae: <i>Erica aristata</i> Andr., <i>E. embotruiifolia</i> Salisb., <i>E. jasminiflora</i> Salisb., <i>E. junonia</i> Bolus, <i>E. praecox</i> Klotzsch, <i>E. shannoniana</i> Andr. Geraniaceae: <i>Pelargonium alchemilloides</i> (L.) L'Her., <i>P. appendiculatum</i> (L.f.) Willd., <i>P. articulatum</i> (Cav.) Willd., <i>P. denticulatum</i> Jacq., <i>P. moniliforme</i> E. Mey. ex Harv., <i>P. oblongatum</i> Harv., <i>P. punctatum</i> (Andr.) Willd., <i>P. radiauum</i> (Andrews) Pers., <i>P. stipulaceum</i> (L.f.) Willd., <i>P. suburbanum</i> Cliff., <i>P. tetragonum</i> (L.f.) L'Hér. Iridaceae: <i>Babiana brachystachys</i> G. J. Lewis, <i>B. spathacea</i> (L.f.) Ker Gawl., <i>Geissorhiza callista</i> Goldblatt, <i>G. longifolia</i> (G. J. Lewis) Goldblatt, <i>G. schinzii</i> (Baker) Goldblatt, <i>G. stenosi-phon</i> Goldblatt, <i>G. tenella</i> Goldblatt, <i>Gladiolus leptosiphon</i> F. Bolus, <i>G. variegatus</i> (G. J. Lewis) Goldblatt & J. C. Manning, <i>Ixia fucata</i> Ker Gawl., <i>I. splendida</i> G. Lewis, <i>Lapeirousia macrospatha</i> Bak., <i>L. simulans</i> Goldblatt & J. C. Manning, <i>L. werecunda</i> Goldblatt, <i>Nivenia argentea</i> Goldblatt, <i>Romulea albiflora</i> Goldblatt & J. C. Manning, <i>Therianthus elongatus</i> (Schltr.) G. J. Lewis, <i>Tritonia bakeri</i> Klatt, <i>T. cooperi</i> (Baker) Klatt, <i>T. lancea</i> (Thunb.) N. E. Br., <i>T. tugwelliae</i> L. Bolus, <i>Watsonia dubia</i> Klatt, <i>W. strictiflora</i> Ker Gawl. Orchidaceae: <i>Disa karoocica</i> Johnson & Linder, <i>D. longicornu</i> L.f., <i>D. marlothii</i> Bolus, <i>D. porrecta</i> Sw., <i>D. salteri</i> G. J. Lewis.]							
<i>Prosoeca ganglbaueri</i> — <i>Pr. robusta</i> pollination system							
Amaryllidaceae							
<i>Brunsvigia</i>							
<i>grandiflora</i> Lindl.	z	p	+	<i>Pr. ganglbauerii</i>	31–42	>10	12
<i>gregaria</i> R. A. Dyer	z	p	+	<i>Pr. ganglbauerii</i>	31–42	>10	12
<i>striata</i> (Jacq.) Aiton	z	p	+	<i>Pr. ganglbauerii</i>	34–36	>10	12

Table 2. Continued.

Species	Flower			Pollinator	Mouth part mm	Floral tube mm	Reference
	Symmetry	Color	Scent				
<i>Nerine</i>							
<i>cf. angustifolia</i> (Baker) Watson	z	p	—	<i>Pr. robusta</i>	ca. 33	>5	12
<i>bowdenii</i> S. Watson	z	p	—	<i>Pr. ganglbaueri</i>	27–30	ca. 5	12
<i>Geraniaceae</i>							
<i>Pelargonium</i>							
<i>carneum</i> Jacq.	z	p	—	<i>Pr. ganglbaueri</i>	34–36	55–60	12
				<i>Pr. longipennis</i>	38–40	55–60	8
<i>dipetalum</i> L'Her.	z	cr/p	—	<i>Pr. longipennis</i>	38–40	ca. 60	8
<i>gracillimum</i> Fourc.	z	p	—	<i>Pr. ganglbauerii</i>	34–36	50–60	12
<i>pinnatum</i> (L.) L'Her.	z	cr/p	—	<i>Pr. longipennis</i>	38–40	50–60	8
<i>Iridaceae</i>							
<i>Gladiolus</i>							
<i>bilineatus</i> G. Lewis	z	p	—	<i>Pr. longipennis</i>	38–40	50–60	8
<i>calcaratus</i> G. J. Lewis	z	w	—	<i>Pr. robusta</i>	20–23	28–40	3
<i>engysiphon</i> G. Lewis	z	cr	—	<i>Pr. longipennis</i>	38–40	52–60	3
<i>macneilii</i> Qberm.	z	p	—	<i>St. wiedmannii</i>	23–29	40–45	3
<i>microcarpus</i> G. J. Lewis	z	p	—	<i>Pr. ganglbaueri</i>	27–30	35–40	3
<i>mortoni</i> Herbert	z	p	—	<i>Pr. ganglbaueri</i>	31–42	36–52	3
<i>oppositiflorus</i> J. D. Hook.	z	p	—	<i>Pr. ganglbaueri</i>	28–32	40–50	12
<i>varius</i> F. Bolus	z	p	—	<i>Pr. ganglbaueri</i> and <i>Pr. robusta</i>	33–35 20–30	45–55 45–55	3 12
<i>Hesperantha</i>							
<i>brevicaulis</i> (Baker) G. J. Lewis	a	p	—	<i>St. wiedmannii</i>	18–30	25–37	12
<i>grandiflora</i> G. J. Lewis	z	p	—	<i>Pr. ganglbaueri</i>	23–25	33–36	12
<i>scapulosa</i> Hilliard	a	p	—	<i>Pr. ganglbaueri</i>	32–35	32–40	12
<i>cf. woodii</i> R. C. Foster	a	p	—	<i>Pr. ganglbaueri</i>	27–31	35–38	12
<i>Nivenia</i>							
<i>stenosiphon</i> Goldblatt	a	b	—	<i>Pr. ganglbaueri</i>	23–25	32–38	10
<i>Tritoniopsis</i>							
<i>revoluta</i> (Burm.f.) Goldblatt	z	p	—	<i>Pr. ganglbaueri</i>	23–25	ca. 40	12
<i>Watsonia</i>							
<i>wilmsii</i> N. E. Br.	z	p	—	<i>Pr. ganglbaueri</i> and <i>Pr. robusta</i>	33–35 36–45	40–45 40–45	12 12
<i>Lamiaceae</i>							
<i>Orthosiphon</i>							
<i>tubiformis</i> R. Good	z	p	—	<i>St. wiedmannii</i>	23–29	28–35	12
<i>Plectranthus</i>							
<i>ambiguus</i> (Bol.) Codd	z	b	—	<i>St. sp.</i>	20–33	22–29	11
<i>ecklonii</i> Benth.	z	ma	—	<i>St. wiedmannii</i>	16–21	24–26	11, 12
<i>hilliardii</i> Codd	z	b	—	<i>St. sp.</i>	21–29	22–29	11
<i>Orchidaceae</i>							
<i>Disa</i>							
<i>oreophila</i> Bolus	z	p	—	<i>Pr. ganglbaueri</i>	19.6(2.3)	20.6(1.1)	5
<i>amoena</i> Linder	z	p	—	<i>Pr. ganglbaueri</i> and <i>Pr. robusta</i>	33–35 20–30	25–30 25–30	12 12
<i>Brownleea</i>							
<i>coerulea</i> Harv. ex Lindl.	z	m	—	<i>St. wiedmannii</i>	ca. 23	20–24	12
<i>macroceras</i> Sond.	z	p	—	<i>Pr. ganglbaueri</i>	19.6(2.3)	38.9(6.4)	5

Table 2. Continued.

Species	Flower			Pollinator	Mouth part mm	Floral tube mm	Reference
	Sym- metry	Color	Scent				
Scrophulariaceae							
<i>Zaluzianskya</i>							
<i>microsiphon</i> (Kuntze) K. Schum.	z	w	—	<i>Pr. ganglbaueri</i>	33–35	30–42	12
[Inferred members of the guild—Acanthaceae: <i>Echolium glabratum</i> Vollesen, <i>Isoglossa cooperi</i> C. B. Cl., <i>Rhinacanthus gracilis</i> Klotzsch, <i>Salpinctium natalense</i> (C. B. Cl.) T. J. Edwards, <i>Siphonoglossa linifolia</i> (Lindau) C. B. Cl. Amaryllidaceae: <i>Brunsvigia</i> spp., <i>Cyrtanthus leptosiphon</i> Snij., <i>C.</i> sp. nov., <i>Nerine filamentosa</i> W. F. Barker, <i>N. krigei</i> W. F. Barker. Caryophyllaceae: <i>Dianthus basuticus</i> Burtt Davy. Ericaceae: <i>Erica cerinthoides</i> L. (pink form). Geraniaceae: <i>Pelargonium acraeum</i> R. A. Dyer, <i>P. caucalifolium</i> Jacq. subsp. <i>caucalifolium</i> , <i>P. ionidiflorum</i> (Eckl. & Zeyh.) Steud., <i>P. transvaalense</i> Knuth. Iridaceae: <i>Geissorhiza fourcadei</i> (L. Bolus) G. Lewis, <i>Gladiolus cataractarum</i> Oberm., <i>G. saxatilis</i> Goldblatt & J. C. Manning, <i>G. scabridus</i> Goldblatt & J. C. Manning, <i>Hesperantha coccinea</i> (Backh. & Harv.) Goldblatt & J. C. Manning, <i>H. curoula</i> Hilliard & Burtt, <i>H. hutchingsii</i> Hilliard & Burtt, <i>H. huttonii</i> (Baker) Hilliard & Burtt, <i>H. pulchra</i> Baker, <i>Nivenia concinna</i> N.E. Br., <i>N. stokoei</i> L. Guthrie, <i>Radinosi-phon leptostachya</i> (Baker) N. E. Br., <i>Tritoniopsis flexuosa</i> (Thunb.) G. Lewis, <i>Watsonia occulta</i> N. E. Br. Lamiaceae: <i>Syncolostemon densiflorus</i> Benth., <i>S. macranthus</i> (Garke) Ashby, <i>S. rotundifolius</i> E. Mey., <i>Thorncroftia longiflora</i> N. E. Br., <i>T. media</i> Codd, <i>T. succulenta</i> (Dyer & Bruce) L. E. Codd. Orchidaceae: <i>Disa rhodantha</i> Schltr., <i>D. saxicola</i> Schltr., <i>Satyrium hallackii</i> Bolus. NOTE— <i>Hesperantha pubinervia</i> Hilliard & Burtt may belong here, but although it does have an elongate perianth tube, the tube itself is extremely narrow, accommodating only the style, and it does not produce nectar.							

Anecdotal observations of long-proboscid flies visiting flowers but no claims for pollination or evidence of pollen transfer to stigmas.

Ericaceae. *Erica junonia* Bolus (?*Ph. rostrata*—E. G. H. Oliver, pers. comm.).

Scrophulariaceae. *Jamesbrittenia fruticosa* (Benth.) Hilliard (*Pr. peringueyi*—Museum record); *Zaluzianskya microsiphon* (*Pr. peringueyi*—Museum record).

Geraniaceae. *Pelargonium alchemilloides* (L.) EHer. (*Ph. rostrata*—Vogel, 1954); *P. denticulatum* (unidentified fly—McDonald in Struck, 1997); *P. suburbanum* (*M. longirostris*—Johnson & Steiner, 1997); *P. tetragonum* (unidentified fly—van Jaarsveld in Struck, 1997).

same site on the insect's body would frequently result in insect visits failing to accomplish pollination as a result of stigma clogging by foreign pollen.

In the *Prosoeca peringueyi* pollination guild pollen deposition on the ventral head or thorax is effected by *Pelargonium* species, on the frons or dorsal thorax by *Lapeirousia* species (normally one or two species of a genus is present at any site), and on the dorsal thorax by *Babiana* species (also normally only one species present at any site) (Manning & Goldblatt, 1996). Pollen of *Hesperantha latifolia*, occasionally part of the guild using *P. peringueyi* as pollinator, is deposited on the lateral and upper ventral thorax. In *P. incrassatum* and *P. sericifolium*, which are sympatric at some sites in Namaqualand and are both pollinated by *P. peringueyi*, pollen contamination is avoided by placement of their respective pollen on the ventral head or ventral thorax of *P. peringueyi*, the result of shorter or longer filaments in these two species.

This pattern is repeated in the *Moegistorhynchus longirostris*–*Philoliche* pollination guild (Manning & Goldblatt, 1997). Pollen deposition on the distal

ventral thorax is effected by *Pelargonium* spp. (either *P. praemorsum* or *P. longicaule*) or *Geissorhiza* spp. (either *G. confusa* or *G. excapa*) and on the proximal ventral thorax or lower head by *P. tabulare*. Deposition on the frons is effected by *Lapeirousia anceps*, the dorsal head or thorax by *Tritonia crispa* at some sites, and by *Gladiolus undulatus*, *G. angustus*, or *L. fabricii* at others. *Ixia paniculata* is unusual in having short stamens held within the mouth of the tube, and its pollen is deposited on the frons around the base of the proboscis. Species of Orchidaceae that have stalked pollinaria are probably not directly involved in competition for pollen deposition, but the number of species of Orchidaceae at any site is usually limited to one.

Pollen deposition in the *Prosoeca ganglbaueri* guild follows this general pattern. For example, anthers of *Brunsvigia*, *Nerine*, and *Pelargonium* spp. brush different parts of the ventral head, thorax, or abdomen, depending on stamen length, while pollen of *Gladiolus* and *Watsonia* species is deposited on the dorsal thorax. Orchid pollinaria are placed near the base of the proboscis. Pollen placement

by *Hesperantha* species, which mostly have symmetrically disposed, divergent anthers, is less well defined but is always on the lateral or ventral parts of a fly's body. Pollen of the important long-proboscid fly plant, *Zaluzianskya microsiphon*, is deposited on the ventral head as the anthers are held at the abaxial side of the mouth of the floral tube.

#### EVOLUTION OF THE SYSTEM

Associated with butterfly pollination by Vogel (1954) in his keystone work on pollination systems in the flora of southern Africa, long-proboscid fly pollination appears to have no direct connection with that strategy. Butterfly and long-proboscid fly pollination have some similarities, notably including plant species with odorless, long-tubed flowers. The two systems are, however, independent of one another, and no species of either group of insects share the flowers of any plant species. Moreover, butterfly pollination in southern Africa (excluding the highly specialized *Aeropetes* butterfly system—Johnson & Bond, 1994) is frequently a part of generalist systems that use other insects, including bees, hopliine scarab beetles, and settling moths (Goldblatt et al., 1995). In the Iridaceae, phylogenetic studies in *Gladiolus*, *Lapeirousia*, and *Sparaxis* show that long-proboscid fly flowers are nearly always most closely related to ancestors pollinated by long-tongued bees (Apidae) (Goldblatt et al., 1995, in prep.; Goldblatt & Manning, 1999). Species of *Gladiolus* pollinated by long-proboscid flies fall in taxonomic sections where long-proboscid bee pollination is ancestral and in which butterfly pollination may not occur. In the only section of *Gladiolus* in which butterfly pollination (by the specialist pollinator, *Aeropetes*) is significant, section *Blandus*, butterfly flowers most likely evolved from long-proboscid-fly-pollinated ancestors (Goldblatt & Manning, 1998). Pollination by the *Aeropetes* butterfly does not occur in *Babiana* or *Lapeirousia*, genera in which long-proboscid fly pollination is especially common, nor in *Ixia* or *Sparaxis*, or *Tritonia*.

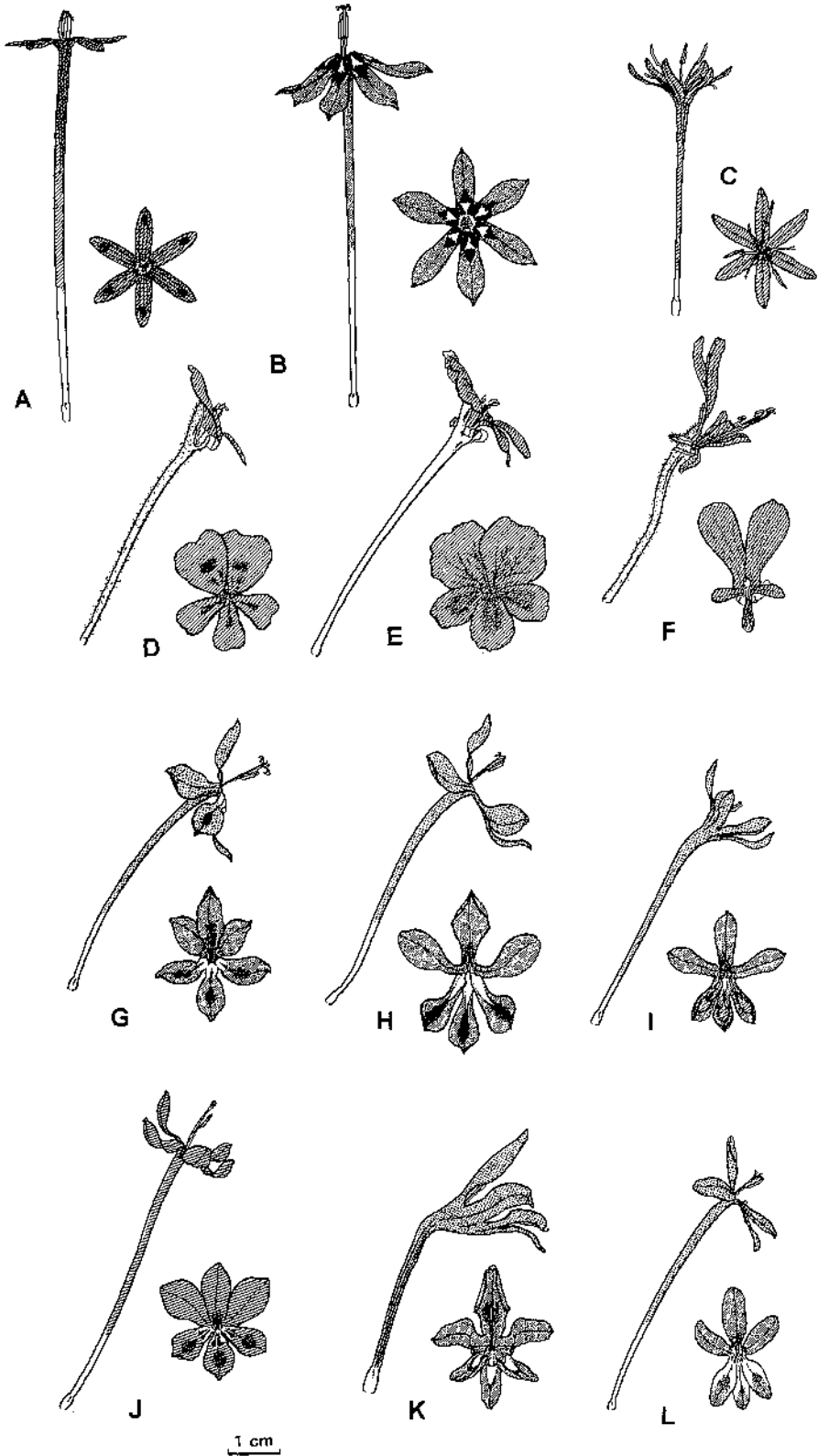
In most families in which long-proboscid fly pollination occurs, a shift from bee to long-proboscid fly pollination appears to be relatively straightforward, involving shifts in perianth color and marking pattern, elongation of the floral tube, and loss of floral odor if present in the ancestor. For example, in most Iridaceae, long-proboscid bee flowers are zygomorphic and have a funnel-shaped perianth tube of moderate length, with the upper flared portion about as long as the cylindrical basal half. Unilateral arcuate stamens are held above the mouth

of the perianth tube where they readily brush against the body of a large bee as it forces its upper body into the upper part of the floral tube while extending its proboscis into the lower part of the tube. The perianth may be almost any color, but is not often red or cream, and the flowers are frequently scented (Goldblatt et al., 1998a). Long-proboscid fly flowers of the *Moegistorhynchus-Philolliche* and the *Prosoeca ganglbaueri* pollination systems merely require a shift in flower coloring toward the pale pink to cream end of the color spectrum, the acquisition of darker, linear nectar guides, and an elongation of the narrow part of the floral tube to exclude nectar feeders with mouth parts less than 15 mm long. Nectar quality, especially sugar constituents, is much the same as is found in long-proboscid bee flowers, but nectar volume is typically much greater and sometimes more dilute. For example, flowers of bee-pollinated species of *Gladiolus* have nectar volumes between 0.5 and 4  $\mu\text{l}$  compared with 1.8 to over 10  $\mu\text{l}$  in long-proboscid fly pollinated species (Goldblatt et al., 1998a; Goldblatt & Manning, 1999).

It is noteworthy that fly diversity is higher in the geographically much smaller winter-rainfall zone. Three fly species range over all of eastern southern Africa, whereas there are 10 fly species in the two long-proboscid fly guilds in the winter-rainfall zone. Some of these flies are relatively widespread, but *Moegistorhynchus* sp. nov. and *Prosoeca* sp. nov., *P. rubicunda*, and *P. nitidula* have very narrow ranges and moreover, except for *P.* sp. nov., they appear to be rare, at least as far as one can judge from the few specimens known.

#### TERMINOLOGY

There is unavoidable confusion when comparing long-proboscid fly and long-proboscid (or long-tongued) bee pollination. Long-proboscid fly pollination, according to our definition, includes flies with probosces in excess of 15 mm and usually much more. Few long-proboscid bees have probosces longer than 12 mm. Moreover, acrocerids, tabanids, and nemestrinids with probosces 10–15 mm long are frequently referred to as long-proboscid flies to contrast them with short-tongue flies that lap fluid. Rebelo et al. (1985) coined the term rhinomyophily, which is useful but not favored by many biologists who prefer more direct terms (e.g., bird pollination vs. ornithophily, etc.). Struck (1997) favored the term hoverfly pollination, but that has the disadvantage of misrepresenting the typical behavior of the flies, which grasp floral organs whenever possible while foraging although





they do hover while inserting the proboscis into a floral tube. We have no solution to offer and suggest *long-proboscid fly pollination* for the syndrome involving flies with probosces usually exceeding 15 mm, and *short-proboscid fly pollination* for the syndrome involving flies with true sucking mouth parts usually less than 15 mm long. Flies with lapping mouth parts would be excluded from this definition. The confusion between long-proboscid fly and long-proboscid bee syndromes as regards length of mouth parts seems unavoidable.

#### NECTAR CONSIDERATIONS

Although most data available for flowers pollinated by Diptera suggest that flies favor nectar with hexose sugars predominant (Baker & Baker, 1983, 1990), these authors did not distinguish between flies with short, lapping mouth parts and those with long, sucking mouth parts. Recent studies, however, show that nectar of plants with flowers adapted for pollination by long-proboscid flies is often sucrose-rich to sucrose-dominant (Goldblatt & Bernhardt, 1990; Goldblatt et al., 1995; Manning & Goldblatt, 1996, 1997; Goldblatt & Manning, 1999). The broader survey here in general confirms this observation, but the data indicate that this may simply be the result of the taxa involved. Most Iridaceae belonging to subfamily Ixioidae (which includes most species pollinated by long-proboscid flies) have sucrose-rich nectar as do all species of the family with flowers adapted for pollination by bees. Significantly, nectar of *Aristea spiralis*, the only species of Iridaceae with long-proboscid fly flowers and not a member of Ixioidae, has hexose-rich nectar. It also produces nectar from perigonal nectaries (Goldblatt & Manning, 1996), unlike species of Ixioidae, which have septal nectaries (Goldblatt, 1990, 1991). Flowers of some other families with long-proboscid fly flowers (e.g., Lamiaceae, Orchidaceae) also have sucrose-rich nectar. However, Geraniaceae does not follow this pattern; species of *Pelargonium* that have been examined (Manning & Goldblatt, 1996, 1997) have, with the exception of *P. cortusifolium*, hexose-rich to hexose-dominant nectar. Among long-proboscid fly flowers then, nectar sugar chemistry may simply be a reflection of systematic affiliation or nectary type, and not the result of selection by long-proboscid flies

for a preferred type of nectar. This reflects the conclusions of van Wyk (1993) and van Wyk et al. (1993) that the nectar sugar characteristics of flowers are highly conserved and that nectar sugar patterns often reflect taxonomic affinities rather than pollination systems.

Nectar concentration is relatively constant, although it seldom rises above 32% sucrose equivalents and seldom dips below 20%. The two species of *Hesperantha* in the *Prosoeca ganglbaurii* guild are exceptional in having nectar concentrations below 20%. Concentrations above 32% may make the nectar too viscous to be easily sucked into the proboscis.

#### A CO-EVOLVED SYSTEM

As suggested by Feinsinger (1983) for sphinx moths, it seems that long-proboscid flies and their flowers have probably evolved through reciprocal selection. Frequent visits from long-proboscid flies select for long-tubed flowers, which in turn select for longer-proboscid flies capable of reaching the nectar within the tubes. This pattern fits the Red Queen effect (van Valen, 1973; Futuyma, 1979), in which species may coevolve indefinitely, some becoming extinct in the process, or else arrive at a static, nonevolving equilibrium. Evolution within this system may not, however, be all that simple. Population densities of long-proboscid flies appear to be highly erratic (Goldblatt et al., 1995; Goldblatt & Manning, 1999), a situation comparable to that for sphinx moths, as noted by Gregory (1963–1964). But whereas shorter-proboscid moths visit these flowers, taking advantage of nectar welling up in the tubes, there do not seem to be alternative shorter-proboscid insects available for most long-proboscid fly flowers to use this resource when their primary pollinators are not available. Instead, those long-proboscid fly flowers that are self-incompatible simply fail to reproduce or reproduce poorly in certain seasons at certain sites (Goldblatt & Manning, 1999).

Fail-safe mechanisms for self-pollination appear to be quite common among species pollinated by long-proboscid flies. We know now that of the ten species of *Lapeirousia* with flowers adapted for pollination by long-proboscid flies, four at least are self-compatible and autogamous and two are self-

←

Figure 4. Representative examples of flower form in species pollinated by the long-proboscid flies of the *Prosoeca peringueyi* pollination guild. —A. *Romulea hantamensis*. —B. *Lapeirousia oreogena*. —C. *Hesperantha oligantha*. —D. *Pelargonium ericifolium*. —E. *P. magentium*. —F. *P. crassicaule*. —G. *Lapeirousia pyramidalis*. —H. *L. dolomitica*. —I. *L. violacea*. —J. *L. silenoides*. —K. *Sparaxis metelerkampiae*. —L. *Tritonia marlothii*.

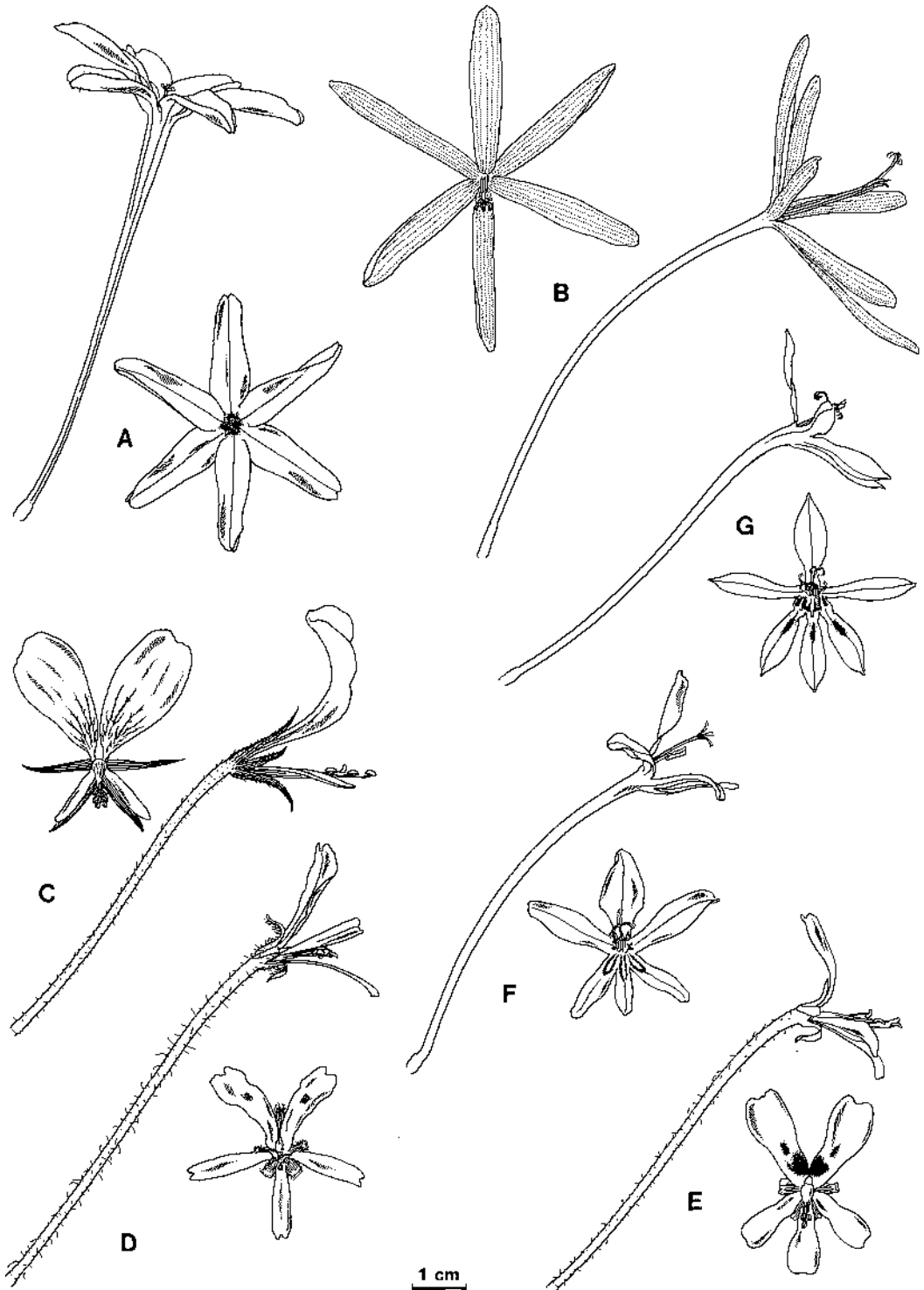


Figure 5. Representative examples of flower form in species pollinated by the long-proboscid flies *Moegistorhynchus longirostris* and *Philoliche gulosa*. —A. *Ixia paniculata*. —B. *Geissorhiza exscapa*. —C. *Pelargonium longicaule*. —D. *P. appendiculatum*. —E. *P. moniliforme*. —F. *Bobiana tubulosa*. —G. *Lapeirousia anceps*.

Table 3. Nectar sugars in species of plants pollinated by long-proboscid flies, including data for some species inferred to belong to this pollinator class. Nectar analyses were provided by B.-E. van Wyk. Species are grouped by pollination system. Standard deviation in parentheses after mean nectar sugar concentration is given only for samples greater than 2. References, column eight, are as follows: 1 = Goldblatt et al. (1995) and Manning & Goldblatt (1997); 2 = Manning & Goldblatt (1997); 3 = Goldblatt & Manning (1999); 4 = Goldblatt et al. (1999); 5 = Johnson & Steiner (1997a); 6 = Johnson & Steiner (1997b); 7 = Struck (1997); 8 = Manning & Goldblatt (1995); 9 = Vogel (1954); 10 = Goldblatt & Bernhardt (1990); 11 = Poigietter et al. (1999); 12 = Goldblatt & Manning (new data, for methodology see Goldblatt et al. (1998a), Goldblatt & Manning (1999)).

Species	Nectar		Range of sugars %				Sucrose/ F + G (n)	Reference
	Volume $\mu$ l (n)	Conc. % (SD)	Fru	Glu	Suc			
<i>Prosoeca peringueyi</i> pollination system								
Iridaceae								
<i>Babiana</i>								
<i>curvica</i>	2.0-4.4 (5)	28.0 (2.0)	9-12	14-19	58-73	1.90 (4)	1	
<i>dreyeri</i>	3.9-9.6 (5)	23.3 (2.2)	13-15	19-21	64-68	1.94 (2)	1	
<i>ecklonii</i>	4.3-8.9 (5)	27.7 (2.0)	5-11	10-18	72-85	3.29 (3)	12	
<i>fiabellifolia</i>	3.9-9.6 (5)	26.8 (1.6)	3-7	10-14	75-79	4.53 (2)	1	
<i>framesii</i>	2.6-6.4 (10)	28.3 (2.2)	7-9	12-14	77-81	3.84 (3)	1	
<i>geniculata</i>	3.2-4.8 (5)	29.3 (1.2)	17	21	62	1.63 (1)	1	
<i>pubescens</i>	3.2-4.8 (5)	28.0 (1.7)	3-8	9-14	78-88	2.18 (2)	1	
<i>sambucina</i>								
var. <i>longibracteata</i>	3.9-6.6 (2)	28-32	6-12	10-19	69-84	3.48 (3)	12	
<i>Hesperantha</i>								
<i>grandiflora</i>	2.8-4.1 (5)	14.8 (1.0)	—	—	—	—	12	
<i>latifolia</i>	0.7-1.1 (10)	23.5 (2.4)	23-29	24-30	41-53	0.94 (3)	1	
<i>oligantha</i>	1.1-1.8 (5)	26.4 (3.9)	19-23	24-25	52-57	1.20 (2)	2	
<i>woodii</i>	1.2-1.8 (5)	18.1 (0.9)	—	—	—	—	12	
<i>Lapeirousia</i>								
<i>dolomitica</i>	1.4-3.1 (5)	30.4 (2.4)	4-9	12-14	77-84	4.13 (2)	1	
subsp. <i>dolomitica</i>	1.5-2.3 (6)	27.3 (2.9)	8	17	75	3.00 (1)	1	
<i>jacquinii</i>								

Table 3. Continued.

Species	Nectar			Range of sugars %			Sucrose/ F + G (n)	Reference
	Volume $\mu$ l (n)	Conc. % (SD)	Fru	Glu	Suc			
<i>oreogena</i>	2.5-7.3 (10)	25.8 (1.6)	11-17	19-25	58-69	1.90 (4)	1	
<i>pyramidalis</i>								
subsp. <i>regalis</i>	2.6-4.8 (10)	28.4 (2.4)	4-21	12-31	48-84	2.45 (6)	1	
<i>sitenoides</i>	1.7-3.6 (10)	26.5 (1.1)	5-8	18-27	65-77	2.45 (3)	1	
<i>violacea</i>	1.4-1.8 (10)	27.0 (2.9)	9-13	15-16	71-76	2.77 (2)	1	
<i>Romulea</i>								
<i>hantamensis</i>	3.7-5.2 (2)	19-21	23	27	50	1.00 (1)	1	
<i>Sparaxis</i>								
<i>meteler-kampitae</i>	1.7-2.2 (6)	28.5 (3.4)	1-12	4-22	70-95	3.23 (4)	1	
<i>Tritonia</i>								
<i>marlothii</i>	2.1-3.5 (5)	29.3 (1.5)	13-14	17-18	68-70	2.23 (2)	12	
Ericaceae								
<i>Erica</i>								
<i>junonia</i>	0.5-1 (4)	22-25	—	—	—	—	12	
Geraniaceae								
<i>Pelargonium</i>								
<i>appendiculatum</i>	1.5-2.1 (2)	23-27	55	45	0	0 (2)	2	
cf. <i>barklyi</i>	2.6-3.2 (6)	25.8 (2.8)	70-78	14-15	7-17	0.14 (2)	12	
<i>moniliforme</i>	1.3-2.2 (2)	19-21.5	50-51	41-42	6	0.06 (2)	2	
<i>longicaule</i>	1.8-3.6 (5)	20.2 (2.6)	48-64	36-40	0	0 (3)	2	
<i>myrrhifolium</i>	2.3-3.6 (5)	20.2 (2.6)	—	—	—	—	12	
<i>patulum</i>	—	—	45-55	35-43	2-20	0.12 (2)	12	
<i>praemorsum</i>	1.3-4.2 (3)	29.3 (0.6)	55	45	0	0 (1)	2	

*Moegistorhynchus-Philobolus* pollination system

Table 3. Continued.

Species	Nectar				Range of sugars %			Sucrose/ F + G (n)	Reference
	Volume $\mu$ l (n)	Conc. % (SD)	Fru	Glu	Suc	Fru	Glu		
<i>Iridaceae</i>									
<i>Aristea</i>									
<i>spiralis</i>	>0.5 (2)	9-11	28-32	35-36	33-36			0.53 (2)	12
<i>Babiana</i>									
<i>brachystachys</i>	5.3-8.2 (5)	23.4 (1.2)	18-19	24-27	54-58			1.28 (2)	2
<i>spathacea</i>	4.3-5.5 (3)	29.3 (1.1)	13-16	16-18	66-71			2.17 (2)	12
<i>tubulosa</i>	4.5-6.2 (10)	24.9 (1.3)	9-15	14-22	63-77			2.57 (3)	2
<i>Geissorhiza</i>									
<i>bonaspei</i>	2.4-4.1 (10)	24.9 (1.4)	14-15	16-19	66-70			2.13 (3)	12
<i>confusa</i>	2.5-4.8 (10)	19.6 (2.2)	17-21	16-18	61-67			1.78 (2)	12
<i>excopa</i>	2.7-3.5 (10)	22.8 (2.7)	16-17	19	64-65			1.4 (2)	2
<i>tenella</i>	2.1-2.8 (5)	24.4 (2.1)	—	—	—			—	2
<i>Gladiolus</i>									
<i>angustus</i>	3.9-9.6 (5)	27.8 (2.2)	1-2	6-11	87-93			9.00 (2)	2
<i>carneus</i>	1.6-2.4 (2)	29.0-31.0	0-7	9-13	80-91			5.89 (2)	3
<i>floribundus</i>	2.8-3.7 (2)	28.0-29.5	—	—	—			—	3
<i>monticola</i>	2.4-4.2 (10)	33.2 (3.6)	3-5	10-14	81-85			5.12 (3)	3
<i>undulatus</i>	6.6-10.6 (3)	25.3 (2.6)	2-3	12	85-86			5.90 (2)	2
<i>vulgatus</i>	2.8-4.2 (4)	29.9 (0.8)	0-5	4-8	87-96			9.71 (3)	3
<i>Ixia</i>									
<i>beltendenii</i>	2.0-2.4 (6)	23.7 (3.3)	14-19	12-22	60-75			1.94 (3)	12
<i>paniculata</i>	3.9-5.7 (8)	26.1 (2.7)	16-19	17-23	58-66			1.66 (3)	2
<i>paucifolia</i>	1.1-1.6 (5)	29.8 (1.8)	17-21	20-25	54-63			1.41 (2)	12
<i>Lapeirousia</i>									
<i>anceps</i>	1.5-2.4 (10)	25.6 (1.7)	6-20	20-26	54-74			1.78 (3)	1, 2
<i>fabricii</i>	1.3-3.4 (10)	32.5 (2.3)	12-21	21-26	53-67			1.15 (4)	1, 2
	2.4-3.1 (10)	26.0 (3.1)	—	—	—			—	
<i>verecunda</i>	0.6-3.0 (10)	26.6 (2.5)	8	18	74			2.85 (1)	1, 2

Table 3. Continued.

Species	Nectar			Range of sugars %			Sucrose/ F + G (n)	Reference
	Volume $\mu$ l (n)	Conc. % (SD)	Fru	Glucose	Suc	Fru		
<i>Tritonia</i>								
<i>crispa</i>	2.4-3.2 (10)	26.1 (4.4)	8-12	11-15	73-81		3.40 (3)	2
<i>flabellifolia</i>	2.3-3.4 (3)	23.2 (1.5)	8-16	11-14	70-81		3.17 (3)	12
<i>pollida</i>	1.5-4.2 (5)	27.7 (1.5)	—	—	—		—	12
Orchidaceae								
<i>Disa</i>								
<i>draconis</i>			no measurable nectar produced					6, 12
<i>harrietiana</i>			no measurable nectar produced					6
Amaryllidaceae								
<i>Cyrtanthus</i>								
<i>sp. nov.</i>	4.5-6.8 (5)	14.0 (2.92)	—	—	—		—	12
Geraniaceae								
<i>Pelargonium</i>								
<i>carneum</i>	1.7-2.4 (3)	26-32	—	—	—		—	8
<i>dipetalum</i>	1.5-1.7 (5)	28.3 (1.7)	—	—	—		—	8, 12
<i>pinnaeum</i>	0.8-2.2 (5)	22.3 (1.5)	—	—	—		—	8, 12
Indaceae								
<i>Cladolus</i>								
<i>bitneatus</i>	4.7-5.6 (3)	27.2 (1.4)	4	11	85		5.67 (1)	8
<i>engysiphon</i>	2.8-4.3 (5)	26.8 (1.4)	0	16	84		5.25 (1)	8
<i>macneilii</i>	4.5-5.8 (5)	26.8 (1.9)	—	—	—		—	3
<i>microcarpus</i>	3.8-4.5 (5)	26.0 (1.1)	—	—	—		—	3
<i>mortoniensis</i>	4.4-5.7 (10)	27.7 (1.6)	5-11	16-19	70-79		2.85 (3)	3
<i>oppositiflorus</i>	6.4-12.8 (6)	27.3 (1.3)	6-8	14-20	74-78		3.17 (2)	12
<i>varius</i>	6.5-8.9 (7)	30.3 (2.4)	2-6	10-18	76-88		4.80 (4)	3
<i>Hesperantha</i>								
<i>grandiflora</i>	2.8-4.1 (5)	14.8 (1.0)	—	—	—		—	12
<i>scopulosa</i>			no measurable nectar produced					
<i>woodii</i>	1.2-1.8 (5)	18.1 (0.9)	—	—	—		—	12

*Prosoeca ganglbaueri-robusta* pollination system

Table 3. Continued.

Species	Nectar			Range of sugars %			Sucrose/ F + G (n)	Reference
	Volume $\mu$ l (n)	Conc. % (SD)	Fru	Glu	Suc			
<i>Nivenia</i>								
<i>argentea</i>	1.6-2.8 (6)	26.7 (2.2)	—	—	—	—	—	—
<i>stenosiphon</i>	ca. 2 (3)	22-38 (n/a)	32	30	38	0.62 (1)	12	12
<i>Radinosiphon</i>								
<i>leptostachya</i>	1.8-2.6 (3)	19.5 (1.3)	—	—	—	—	—	12
<i>Tritoniopsis</i>								
<i>renoluta</i>	2.3-2.9 (2)	30-34	23	17	60	1.5 (1)	12	12
<i>Watsonia</i>								
<i>wilmsii</i>	2.8-4.3 (4)	26.3 (0.9)	4-17	16-22	61-89	2.51 (4)	12	12
<b>Lamiaceae</b>								
<i>Orthosiphon</i>								
<i>tubiformis</i>	2.7-4.1 (10)	24.5 (2.2)	0-1	0-5	94-100	25.20 (3)	12	12
<b>Orchidaceae</b>								
<i>Brownliea</i>								
<i>coerulea</i>	1.3-1.8 (2)	25-27	10	0-11	79-90	5.45 (2)	12	12
<i>macroceras</i>	2.8-4.6 (5)	27.5 (3.3)	—	—	—	—	12	12
<i>Disa</i>								
<i>amoena</i>			no measurable nectar produced				5	
<b>Scrophulariaceae</b>								
<i>Zabuziana</i>								
<i>Zabuziana</i>								
<i>microsiphon</i>	2.6-4.3 (5)	32.6 (1.2)	—	—	—	—	12	12

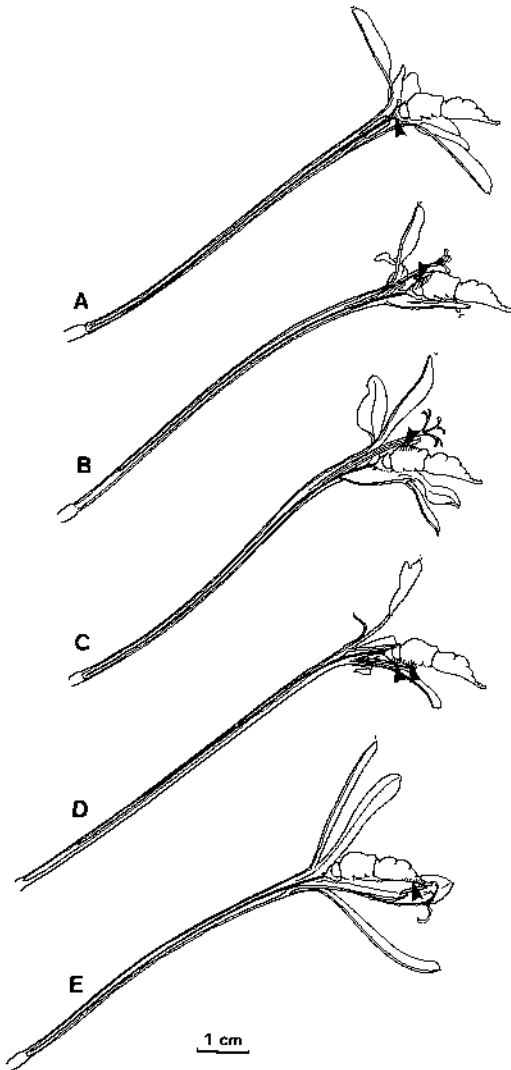


Figure 6. Differential pollen deposition on the body of a fly in a guild of plant species pollinated by *Moegistorhynchus longirostris*. —A. *Ixia paniculata* (frons and proboscis base). —B. *Tritonia crisa* (dorsal thorax). —C. *Lapeirousia fabricii* (dorsal thorax). —D. *Pelargonium appendiculatum* (ventral thorax). —E. *Geissorhiza exscapa* (ventral abdomen).

incompatible (Goldblatt et al., 1995, and unpublished data). At least one species of *Hesperantha* (*H. latifolia*) and the *Ixia* and *Sparaxis* species known to be pollinated by long-proboscid flies are facultatively autogamous, whereas in *Gladiolus* self-incompatibility appears to be frequent (Goldblatt et al., 1998a, in prep.). Some populations of *Gladiolus* species with long-proboscid fly flowers have set no capsules for three years for which we have observations when their pollinators were absent. Al-

though in *Pelargonium* self-compatibility appears to be the rule (Struck, 1997), autogamy cannot normally take place because of mechanical protandry. There is therefore no barrier to geitonogamous pollination in this genus in which inflorescences produce numerous flowers contemporaneously but pollination must be mediated by an external agent.

Proboscis length is typically shorter than the floral tube, a feature that long-proboscid fly pollination shares with sphinx moth pollination. This ensures that a visiting insect must push its body into flowers so that its proboscis will extend as deeply as possible into the tube and reach the nectar reservoir. Orchid genera are one notable exception. In deceptive flowers of *Disa amoena* and the *Disa draconis* complex (Johnson & Steiner, 1997), spur lengths may be shorter than the proboscis length and pollinaria are attached to the upper third of the proboscis. Other exceptions are *Aristea spiralis* and species of *Brunsvigia* and *Nerine* that are pollinated by long-proboscid flies; in these taxa floral tubes are less than 10 mm long. These flies, however, have bodies large enough and probosces long enough that they will consistently brush against anthers and accumulate deposits of pollen on their ventral thoraces and abdomens. Nectar produced by such short-tubed flowers is obviously accessible to a range of other insects, and we have observed effective pollination by bees in *Aristea spiralis*. We have not recorded visits to any other of these short-tubed species by insects other than long-proboscid flies. The considerable distance of the anthers from the mouth of the tube also makes it unlikely that even large bees would normally contact anthers when foraging for nectar in such flowers because their bodies are so much shorter than the filaments.

#### LONG-PROBOSCID FLY POLLINATION IN THE HIMALAYAS

Attention was first drawn to long-proboscid fly pollination in Asia by Fletcher and Son (1931), who briefly described visits to (and inferring pollination of) *Roscoea purpurea* (Zingiberaceae) by the tabanid fly *Chorizoneura longirostris* (proboscis 50–60 mm long). Subsequently, Dierl (1968) described in detail the behavior of this fly in the course of its visits to flowers (presumably foraging for nectar) on *Roscoea*. The Himalayan region is floristically rich and includes several plant species with long-tubed flowers that may also be pollinated by this fly, e.g., other species of *Roscoea* and *Rhododendron* spp. (Ericaceae). This pollination guild awaits more extensive investigation. Involving different fly genera and plant species, the Himalayan system presum-



ably evolved independently of the long-proboscid fly guilds of southern Africa.

#### TAXONOMIC DISTRIBUTION OF LONG-PROBOSCID FLY POLLINATION

According to our survey, at least 83 species have been shown to be pollinated solely by long-proboscid flies. Based on their nearly identical floral presentation, it seems reasonable to infer that at least 90 more species also have this pollination strategy. Even if this figure is grossly underestimated, there seems no doubt that long-proboscid fly pollination is of relatively minor importance in the flora of southern Africa, which comprises over 20,500 species of flowering plants (Goldblatt, 1997). Nevertheless, long-proboscid fly pollination assumes more than marginal importance in at least two families in southern Africa, Geraniaceae and Iridaceae. Precise figures are not available for Geraniaceae, but Struck (1977) has estimated that 25% of the southern African species of *Pelargonium* are pollinated by long-proboscid flies, although the exact definition of the system that he entertained is not clear. In Iridaceae we have more accurate figures. Some 105 of the approximately 1025 species in southern Africa appear to have this pollination system exclusively and one or two more (e.g., *Hesperantha coccinea*—S. D. Johnson, pers. comm.; *Aristea spiralis*, *Watsonia borbonica*—Table 2) may have a combined long-proboscid fly and other insect pollination. Thus, about 10% of southern African Iridaceae have adopted this pollination strategy. This is substantially more than the estimated 64 species (6.3%) of the southern African Iridaceae that are predicted on the basis of floral morphology to be pollinated by sunbirds (Goldblatt et al., 1999a).

Among the Iridaceae, long-proboscid fly pollination appears to be most well developed in *Lapeirousia*, in which 10 species, or 30% of the total in temperate southern Africa, have flowers pollinated by long-proboscid flies. The system is also well developed in *Gladiolus* (Goldblatt & Manning, 1999; Manning & Goldblatt, 1999), in which 27 species are considered to have flowers adapted for this particular pollination strategy (17% of the southern African species), and long-proboscid fly pollination is inferred for between 10 and 20% of the southern African species of five other large genera, *Babiana*, *Geissorhiza*, *Hesperantha*, *Ixia*, and *Tritonia*.

Long-proboscid fly pollination assumes more modest importance in Ericaceae (Rebello et al., 1985) and Orchidaceae, although prominent in

*Brownleea* and *Disa*, and we have yet to assess its significance in Amaryllidaceae and Lamiaceae. The strategy seems likely in Acanthaceae, but it has yet to be confirmed in that family. In the remaining families in which it occurs, long-proboscid fly pollination is decidedly rare and is evidently confined to just one or a few species. Curiously, evolution of the system seems highly labile in several genera of the Iridaceae and in *Disa* (Orchidaceae). In *Disa* and *Gladiolus* it has evolved repeatedly in different lineages (Johnson et al., 1998; Goldblatt & Manning, 1999), an estimated nine times in the latter genus.

#### CONSERVATION

Long-proboscid fly pollination poses important concerns for conservation. Plants pollinated by a single insect, or no more than two over their entire range, clearly are at more significant risk than those that are pollinated by several different insects (Bond, 1994). Long-proboscid flies may be regarded as keystone species, for several plant species depend on particular flies for their pollination and sexual reproduction. Conservation of plants with these specialist pollinators must involve conservation of their pollinators, an undertaking fraught with unusual difficulties. Both Nemesstrinidae and Tabanidae have complex life cycles. Tabanidae have carnivorous, aquatic larvae that require wetland habitats for their larval development, which may take place some distance from sites of the plant species on which the adults feed. Female tabanids also require a blood meal during their adult phase before egg-laying can proceed. This makes the presence of suitable host mammals essential. Nemesstrinidae have an equally complex life history. Although no details of the life cycles of long-proboscid flies are known, all members of the Nemesstrinidae so far studied have parasitic larvae, often on locusts. Obviously, large, relatively undisturbed sites with a diversity of habitats are necessary for the completion of the life cycles of nemesstrinids and tabanids.

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