CUPID COMES IN MANY GUISES

The not-so-humble fly and a pollination guild in the Overberg.

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The vast majority of flowering plant species require pollination in order to produce seeds. Pollination is mostly carried out via an animal intermediary or vector. With few exceptions these are flying insects, usually bees, butterflies or moths, and true flies.

Flies? Actually fly-pollination is not uncommon and is achieved in various ways. A number of milkweeds (Asclepiadaceae) and aroids (Araceae) attract carrion flies (families Calliphoridae and Muscidae) by emitting a foul odour reminiscent of putrid flesh. A variety of flies are also attracted to the rather musty-smelling clumps of small white flowers produced by some forest trees, including milkwoods, and by garden rhubarb.

However, unattractive odours and at best nondescript appearance are not inevitable in fly-pollinated flowers. Many plant species attract nectar-feeding flies, particularly in the families Acroceridae, Bombylliidae, Nemestrinidae and Tabanidae. Although all of the fly species in this group have some sort of elongated proboscis, it is in the tangle-veined flies and horse-flies that they reach remarkable lengths: up to 70 mm long in some instances. Such long-tongued flies are unusually well represented in South Africa, and are especially diverse in the Cape Floral Region and Namaqualand.

Long-tongued flies

The family Tabanidae (horse-flies) is well represented in South Africa, with a total of 227 species in 19 genera. They are most common in the wetter parts of the country, both in the summer and winter rainfall regions. The adults of both sexes feed on the nectar and pollen of flowers, although the females of most species also suck blood. The mouthparts are usually short, and flowers without or with a short floral tube are
visited. In some species, however, the mouthparts are developed into a distinct proboscis. This is most pronounced in the genus *Philolicle*. Although usually shorter than the body, in two Cape species, *P. rostrata* and *P. gulosa*, the proboscis is rather longer (15-25 mm). These species have both been recorded pollinating *Disa draconis*, which has cream-coloured flowers marked with maroon streaks in the mouth and a long spur. We have collected *P. gulosa* on *Lapeirousia fabrictii*, which also has cream or flesh-coloured flowers with purple streaks and a long floral tube.

The family Nemestrinidae (tangle-veined flies) is represented in South Africa by 48 species in 6 genera. The adults are seldom seen but may be quite common at certain localities at the right time of the year. They are usually encountered hovering over blossoms or in open sunny patches, and feed on nectar. The mouthparts in many are developed into a proboscis, usually rather shorter than the body, but in some species of the genera *Prosoeca* and *Moegistotrichus* the proboscis is of prodigious length and may be more than four times longer than the body (40-70 mm). In total some 10 or 11 species of tangle-veined flies with a proboscis longer than the body are recorded from South Africa. Only 2 of these are found outside the southern and south-western Cape and Namaqualand.

In this article we restrict the use of the term long-tongued fly to those species with a proboscis 20 mm or more in length, acknowledging that in fact most nectar drinking flies have tongues less than 10 mm long. The importance of long-tongued flies in the pollination ecology of the Cape is underlined by this strong regional concentration. Out of some 12-13 fly species with a proboscis 20 mm or more long, 10-11 of these are restricted to the Cape, specifically the Cape Floral Kingdom and Namaqualand.

**The floral syndrome**

In our studies on pollination of *Lapeirousia* (family Iridaceae) in South Africa, we have discovered that the flowers visited by long-tongued flies can be divided into two groups, the generalists and the specialists. The generalists are not visited solely by these long-tongued flies and are probably seldom actually successfully pollinated by them because the floral tube is too short to allow the anthers or stigma to contact the insect body. They provide a nectar source for these flies but the actual pollination is achieved by various other insects with shorter tongues, such as short-tongued nemestrinids, bees or bee flies (Bombyliidae). The flowers in such species are of
various shapes and colours, concordant with the preferences of their legitimate pollinators.

The second group of plants, the specialists, are actually pollinated by the long-tongued flies, and their very long floral tubes effectively preclude other insect species from obtaining the nectar. One group of these specialist flowers displays a rather consistent suite of floral characters. The flowers are cream to salmon pink, mostly with discrete red or maroon spots, streaks or splashes in the mouth or throat of the long floral tube, and are usually scentless. Nectar is usually produced as the floral reward. The flowers occur singly or in low numbers on the stem, and may exhibit closing movements in the evening. Such a suite of characters is said to define a floral syndrome.

The floral guild
Furthermore it has struck us that such flowers seldom if ever occur in isolation and invariably one or two other plant species with similar flowers will be found in the same area. When this occurs, the plant species exhibiting the same floral syndrome are said to constitute a guild. The formation of guilds is beneficial to both pollinator and plant. For the former it means that an adequate supply of nectar is available throughout the life of the adult fly, even if the flowering periods of individual guild members is shorter. For the plant it means that a reliable and efficient pollinating species can be supported: a pollinator that will carry pollen of only a limited number of plant species, and which will visit these species preferentially.

While collecting plants of *Gladiolus engysiphon* and *G. bilineatus* in the Langeberg, both of which exhibit the long-tongued fly syndrome, we were therefore not surprised to find growing with them species of pelargonium which showed the same floral syndrome. In two sites we found *G. engysiphon* growing with *P. pinnatum* and *P. dipetalum* and at one site *G. bilineatus* growing with *P. pinnatum* and *P. carneum*.

The fly, *Prosoeca longipennis*, responsible for pollinating a variety of species of *Gladiolus* and *Pelargonium* in the southern Cape in autumn.

The species are strikingly similar in flower colour and marking and in the length of the floral tube and they all secrete nectar. These 5 species of *Gladiolus* and *Pelargonium* thus constitute an autumn guild* in the Langeberg, and we were very keen to find the pollinator involved.

The pollinator
Our hopes were realized when we collected the tangle-veined fly *Prosoeca longipennis* visiting *Gladiolus bilineatus*. It is a large, handsome insect with a body length of some 20 mm and a proboscis twice as long. By examining the pollen load on the insect we were able to ascertain that it also visited the pelargoniums at that site. This was particularly easy as each of the 3 guild species at the site have pollen of a different colour. Our insect had a heavy deposit of purple pollen on the top of the thorax, yellow pollen on the underside of the head and thorax, and red pollen on the underside of the thorax. We confirmed that the purple pollen was that of *Gladiolus* and the red and yellow from *Pelargonium* by examining it closely under the microscope.

One of the problems faced by multiple users of the same pollinator, as occurs within a floral guild, is the potential for pollen contamination (the deposition of pollen from one species onto the stigma of a different species). This is even worse than no pollen at all because the foreign pollen can clog the stigma and prevent it from receiving pollen from the same species on a subsequent visit by the pollinator.

Members of this guild overcome the problem by depositing their pollen on different parts of the pollinator. This is achieved by the particular position of the stamens (see accompanying diagram).

Further fieldwork is necessary to establish the generality of our initial observation. We also need to determine whether or not hybridization between the various pelargoniums and gladioli is possible. We did notice that not all of the flowers of either genus set seed, which indicates either some degree of self-incompatibility or at least an inability to self-pollinate. Furthermore, we did not observe any hybrids in either of the genera.
Keystone species
Pollinators can be important determinants of floral characteristics. This is especially evident in the tube length in species of *Pelargonium*. The length of the flower tube is rather variable in species of *Pelargonium*, especially in those which are widespread. For instance, in *P. pinnatum* the tube is 10-60 mm long (forms with the longest tubes are from the southern Cape), in *P. carneum* it is 30-80 mm long, and in *P. dipetalum* it is usually 7-18 mm long. In a few populations of *P. dipetalum* from the southern Cape, including ours, the tube is exceptionally long. It seems evident that this is because tube length in the flower is tracking tongue length in the pollinator. In the case of *P. dipetalum* the more westerly, short-tubed, populations cannot be pollinated by *Prosoeca longipennis*, but must be visited by some other insect with a shorter tongue. Clearly it is the particular length of the proboscis of *P. longipennis* near Riversdale that has caused the remarkable convergence in tube length in the 5 plant species that it pollinates.

The existence of pollination guilds highlights the importance of certain species above others in an ecosystem. Should the pollinator of this guild be driven to extinction, the fate of all five flower species would follow a similar course since they are utterly dependent on it for setting seed. Species such as *Prosoeca longipennis*, which have an inordinately significant impact on their ecosystems, are known as keystone species. The identification of such species is vital if the ecosystem is to be preserved. Similar keystone species will be involved in each of the other long-tubed fly guilds which exist (we know of at least four).

Who would have thought that a few flies could be responsible for maintaining such a wealth of floral splendour.

PLANTS AND POLLEN PLACEMENT
The various plant species which co-occur at any one site deposit their pollen on different parts of the same insect. In *Gladiolus bilineatus* (A) the anthers occur in the upper hood of the flower and contact the upper surface of the insect thorax. In *Pelargonium pinnatum* (D) the anthers are held close to the mouth of the tube on short filaments and brush the face of the fly. In *Pelargonium carneum* (E) the anthers are held out from the flower on long filaments and brush the underside of the body. However, both *Gladiolus* (A and B) species will deposit their pollen on the same part of the fly, and a similar problem is evident in the case of *P. carneum* (E) and *P. dipetalum* (C). Although we never encountered these pairs of species at the same site, we only studied three sites. Although the floral tubes are longer than the pollinator proboscis, the nectar rises by capillary action up the tube to a level where it becomes accessible to the fly, but only just (arrow). It is to the benefit of the plant species if the insect needs to visit many flowers before its appetite is satiated.

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The photograph of *Prosoeca longipennis* was kindly taken by Colin Patterson-Jones.

Further reading

*A table of the floral characteristics of the 'guild members' is available from the author. Please send a stamped, self-addressed envelope to the Executive Officer, Botanical Society, Kirstenbosch, Claremont 7735, tel (021) 797 2090 or fax (021) 797 2376."