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Notes on the pollination of the perfume flowers of *Gloxinia perennis* (Gesneriaceae) by euglossine bees

Notas sobre la polinización de las flores perfumadas de *Gloxinia perennis* (Gesneriaceae) por abejas euglossine

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Abstract: During a field course held at the "Tropenstation La Gamba" 2005, the pollination of cultivated *Gloxinia perennis* (Gesneriaceae) was studied. The flowers provide fragrance as a floral reward for male euglossine bees. Three species of euglossine bees (*Eulaema meriana*, two *Euglossa* species of different size) were observed to visit the flowers, all collecting the fragrance in the usual way. However, only *Eulaema meriana* was large enough to touch the anthers and stigma and proved an effective pollinator. Flower visitation by *Eulaema meriana* was in the early morning, starting with dawn and lasting for approximately one hour. No overlap with visitation of other bees was observed. The bees seem to follow a "first come, first served" strategy. The *Euglossa* species visited the flowers in a staggered way in the subsequent morning hours, with some overlap. The time of visitation and back-loading of the collected fragrance was closely linked with the species and size of the bees. From earlier and the present observations, it may be concluded that the flowers of *Gloxinia perennis* are specifically adapted to the pollination by *Eulaema* bees, even though the fragrance is not specifically addressed to them.

Key words: Gesneriaceae, *Gloxinia perennis*, Apidae-Euglossini, *Eulaema*, *Euglossa*, pollination, perfume flowers.

Resumen: Durante un curso práctico realizado en al "Estación Tropical La Gamba" se estudió la polinización de *Gloxinia perennis* (Gesneriaceae). Las flores proporcionan una fragancia como recompensa floral para los machos de las abejas euglossine. Tres especies de abejas euglossine (*Eulaema meriana* y dos especies de *Euglossa* de diferente tamaño), fueron observadas visitando las flores, todas recolectando la fragancia de la forma habitual. Sin embargo, sólo *Eulaema meriana* fue lo suficientemente grande como para tocar las anteras y el estigma y demostró ser eficaz como polinizador. La visita de flores por *Eulaema meriana* fue temprano en la mañana, a partir de la madrugada y durante aproximadamente una hora. No se observó superposición con las visitas de otras abejas. Las abejas parecen seguir una estrategia de "primero en llegar – primero en servir". Las especies de *Euglossa* visitaron las flores en forma escalonada en las siguientes horas de la mañana, con cierta superposición. El tiempo de visita y transferencia a las patas traseras de la fragancia demostró estar estrechamente vinculada con la especie y el tamaño de las abejas. De observaciones anteriores y actuales se puede concluir que las flores de *Gloxinia perennis* están específicamente adaptadas a la polinización por abejas *Eulaema*, aunque la fragancia no está específicamente dirigida a ellas.

Palabras clave: Gesneriaceae, *Gloxinia perennis*, Apidae-Euglossini, *Eulaema*, *Euglossa*, polinización, flores perfumadas.

Introduction

Excursions of Austrian students to Central America regularly include field courses held at the "Tropenstation La Gamba". In these courses, the students are introduced to field research and have to work out a specific topic. The topics range from floristic to ecophysiological work and includes pollination studies of plants of the Golfo Dulce area.

The present account describes an example of such anthecological studies conducted at the *Tropenstation* (2005): the pollination of *Gloxinia perennis* by euglossine bees.

Gloxinia perennis was among the first plants – and the first case in the dicotyledons – recognised to produce fragrance as a floral reward (VOGEL 1966). VOGEL (l.c.) found that the flowers do not possess a nectary, but an osmophore at the base of the broad corolla tube. He observed and documented visitation and pollination by the euglossine bee *Eulaema nigrita* in north-eastern Brazil. He also reported an observation of R. DRESSLER who noticed *Eulaema meriana* on *Gloxinia perennis* flowers in Panama.

So far, no information is available about whether the flowers are attractive to other euglossine bees and if these are capable of effecting pollination.

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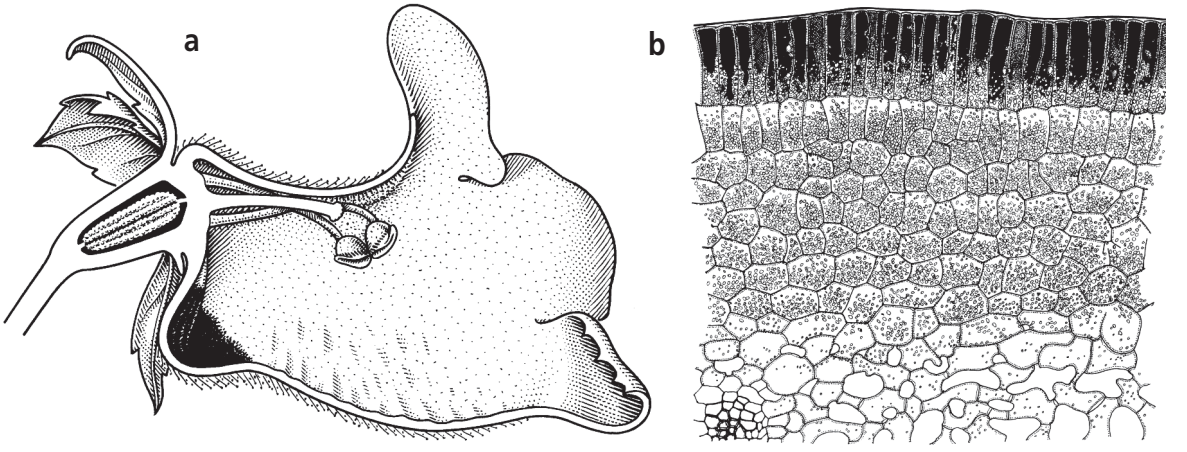

Fig. 1: *Gloxinia perennis*, (**a**) flower in longitudinal section; (**b**) section through the osmophore. (From VOGEL 1966).

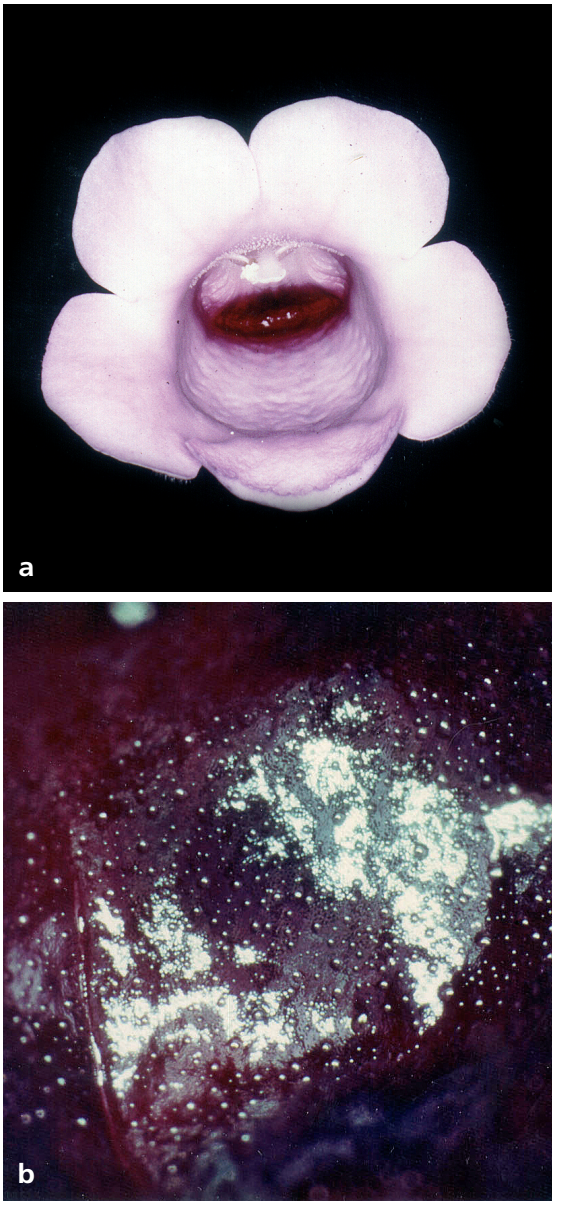

Fig. 2: *Gloxinia perennis*, (**a**) flower in front view, note reddish-brown osmophore at the base; (**b**) surface of osmophore, note terpene droplets.

Study site and methods

The present observations refer to plants cultivated in the garden of the "Tropenstation La Gamba". Euglossine bees, which live in the nearby forest, regularly visit the flowers in the garden. Two students (G.W. and E.H.) were posted near the plants, with the task of recording flower visititation and the duration of certain activities of the bees. Documentation was by photographs and by films (W. HÖDL). A pair of flowers was selected, marked and observed over two days.

Results

Gloxinia and *G. perennis* – general remarks

Gloxinia, described by L'HÉRITIER in 1789, was believed to be monospecific for a long time (e.g., FRITSCH 1893-94). In the last 30 years, the genus has undergone major re-organisation. For some time it has been considered to comprise some 15 species, distributed in Central and tropical South America, with its greatest diversity in Bolivia and Brazil (WIEHLER 1976, 1983). In this wide definition, the genus includes species exhibiting different pollination syndromes, such as melittophily (nectar flowers visited by various bees, including male and female euglossine bees), andro-euglossophily (perfume flowers, visited by male euglossines) and ornithophily (bird-pollinated flowers, e.g., *G. sylvatica*). Based on recent molecular studies, *Gloxinia* was divided into no fewer than six genera (*Gloxinia* s.str., *Gloxiniopsis*, *Mandirola*, *Nomopyle*, *Seemannia* and *Sphaerorrhiza*) (ROALSON et al. 2005a, b). In this narrow sense, *Gloxinia* includes only three species.

Gloxinia perennis has a wide distribution, ranging from Brazil to Panama and Costa Rica. In the latter countries, however, it may be only naturalised (SKOG 1979). One pre-requisite of the wide distribution and naturalisation is the presence of appropriate pollinators.

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Flower morphology

The morphology and anatomy of the flowers of *Gloxinia perennis* have been described and illustrated by VOGEL (1966) (for a brief semi-popular survey see VOGEL et al. 2005). The flowers are campanulate, c. 3 cm long and have a broad, ca. 2.5 cm wide tube. The nectary is completely reduced and functionally replaced by an osmophore situated at the base of the corolla tube (Fig. 1a, 2a). Anatomically, the osmophore consists of palisade-like epidermal cells that secrete tiny droplets of terpenes, and a thick layer (of ca. 8 cell layers) of parenchyma cells densely stuffed with starch grains (Fig. 1b). During emission of the fragrance, the starch gradually disappears and is apparently involved in the synthesis of the fragrant substances (at least it provides the required energy). The surface of the osmophore is purple-brown, smooth and shiny (Fig. 2a). The terpene droplets are only visible with a strong lens (Fig. 2b). The anthers of the four stamens are coherent and held as a small platform just below the corolla roof. The anthers ripen first (protandry) and the pollen is released on the lower side of the anther plate. Afterwards, by growth of the style, the stigma is brought into a position shortly ahead of the anthers. The mouth-like (stomatomorphic) stigma curves down and become receptive. Pollen deposition is thus nototribic.

Visitation by euglossine bees

Number and kinds of bee visitors. Three species of euglossine bees were observed visiting the flowers regularly: *Eulaea meriana* and two unidentified species of *Euglossa*, one large ("*Euglossa* 1") and one small ("*Euglossa* 2") (Fig. 3, 5, 6). The *Euglossa* bees exhibited the typical metallic body colours, while *Eulaema meriana* resembles strongly a large-sized bumblebee (length c. 5 cm), with black head, thorax and legs, and an abdomen with black and white stripes at the base and with rusty brown hairs at the end (Fig. 5).

Visitation times. The first to visit the flowers on a day were the *Eulaema* bees. The first ones arrived at the flowers exactly at the onset of dawn (ca. 5.00 a.m.). The flight is accompanied by a strong flight noise, which is audible from a considerable distance. Visitation was almost exclusively between 5.00 and 6.00 a.m. The next visitors were *Euglossa* 2 bees, the small euglossine bee. They visited the flowers from 7.00 to 9.00 a.m., without any overlap with *Eulaema* bees. The first *Euglossa* 1 bees arrived at ca. 8.00 a.m., with an overlap with *Euglossa* 2 of about one hour. Visitation continued until 11.00 a.m. On the rest of the day, scarcely any bees appeared at the *Gloxinia* flowers.

The observation that *Eulaema meriana* visits the *Gloxinia* flowers only at daybreak is in contrast to the re-

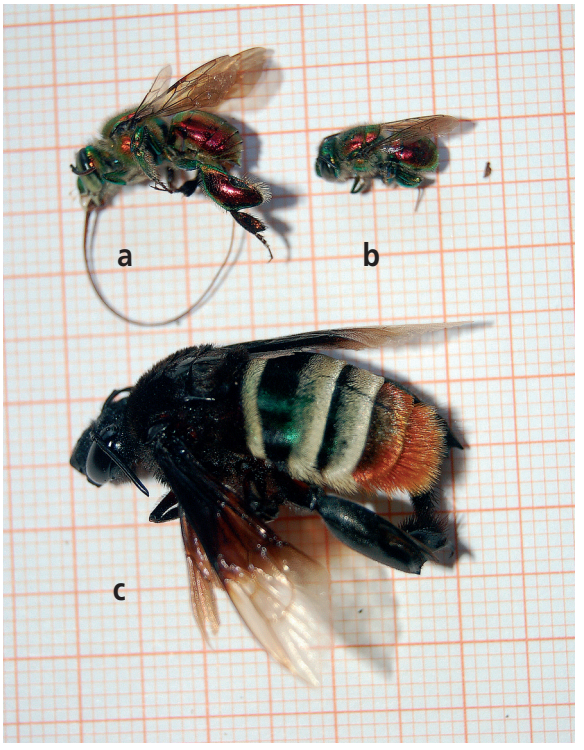

Fig. 3: The three bee species observed visiting the flowers of *Gloxinia perennis*; (**a**) *Euglossa* 1 (large); (**b**) *Euglosa* 2 (small); (**c**) *Eulaema meriana*.

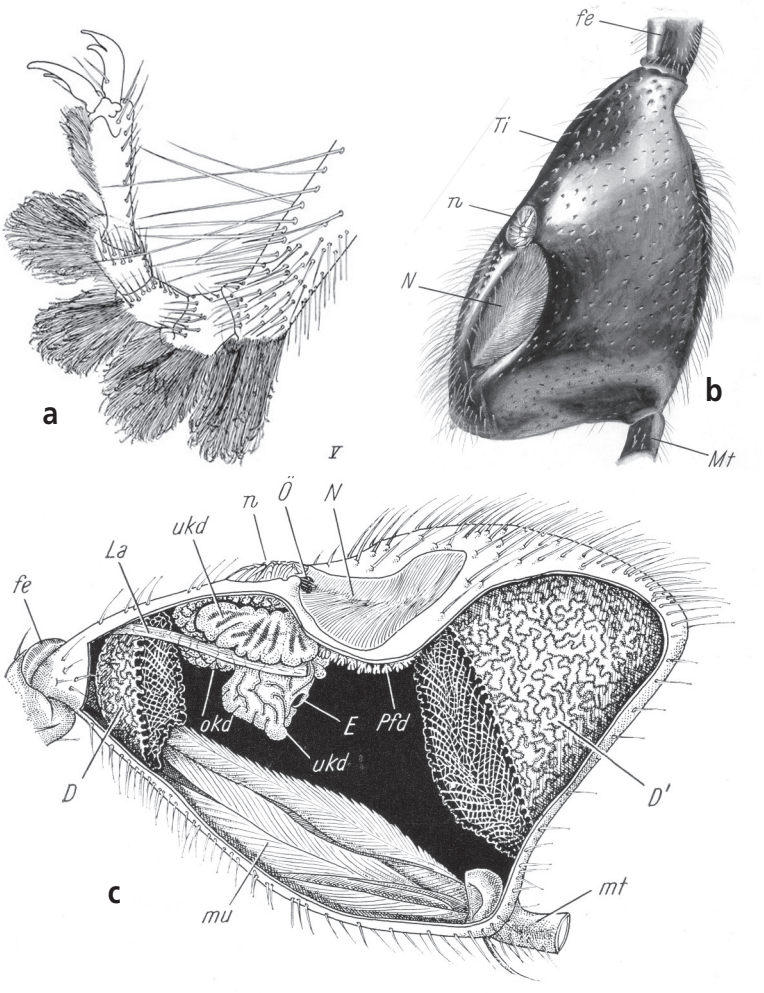

Fig. 4: Tarsal brush (**a**) and tibial organ (**b**, **c**) of an euglossine bee. (From VOGEL 1966).

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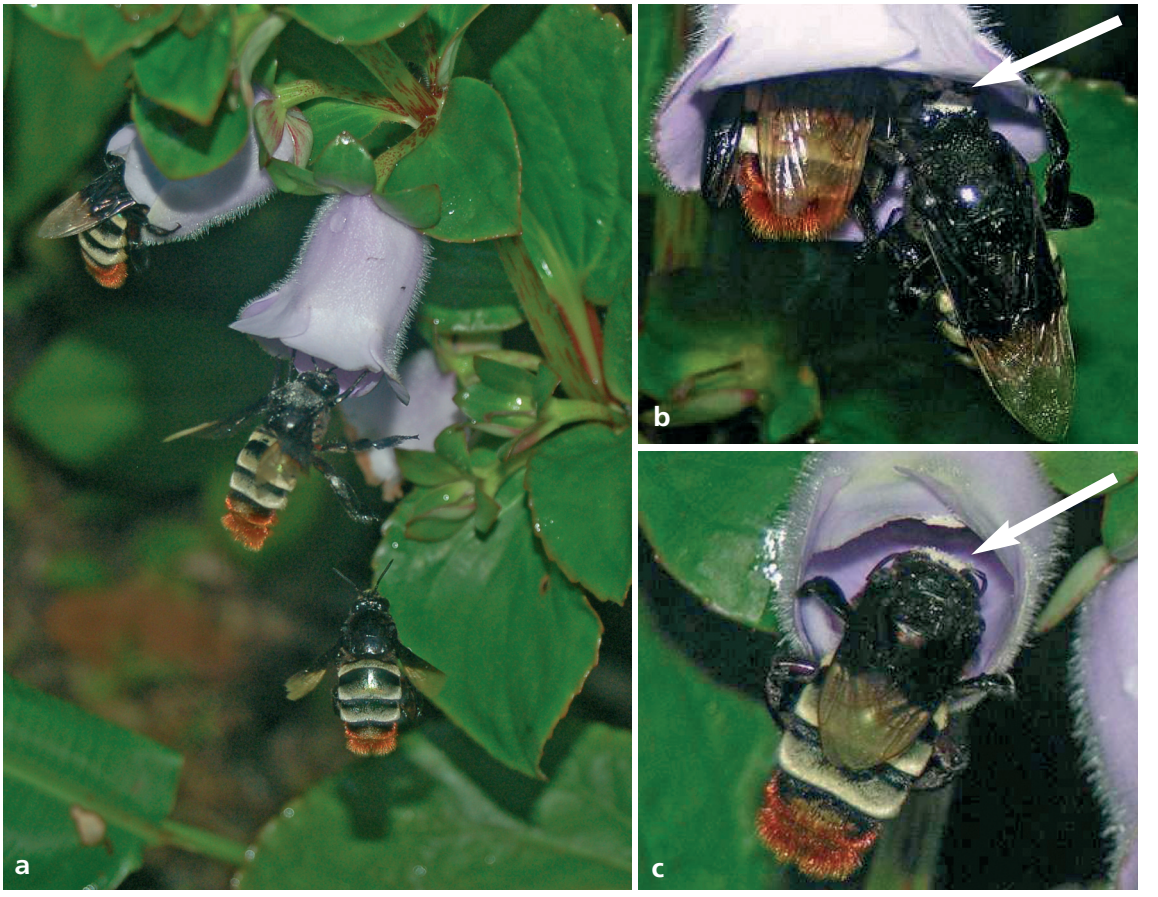

Fig. 5: *Eulaema meriana* visiting the flowers of *Gloxinia perennis*, note pollen deposition on the bee's head in **b** and **c** (arrows).

port of VOGEL (1966) regarding *Eulaema nigrita* in Brazil. He observed the bees at all times of the day (and up to five individuals at a time).

Number of flower visitors. The presence of *Eulaema* bees followed roughly a Gaussian curve, with the peak (5 bees at a time) between 5.30 and 5.40 a.m. The visitation of *Euglossa* 2 (7.00-9.00 a.m.) was less regular, but also with a peak (3 bees) in the middle of the visitation period (7.40-8.20 a.m.). "*Euglossa* 2" showed the least consistency. In the visitation period (8.00-11.00), there were long gaps, and a single bee turned up between 10.00 and 11.00 at intervals of ca. 10 minutes.

Collection process. As is well known from the first description of VOGEL (1966), the male euglossine bees collect the fragrance with their forelegs, the tarsi of which are modified into brushes (Fig. 4a). They wipe the surface of the osmophore with the tarsal brushes. During a short upflight, they load the collected fragrance via the middle leg into the tibial organs of the hind legs (Fig. 4b,c). They then alight again on the flower and continue brushing.

Time spent in the flower (duration of collection activity). *Eulaema* spent the longest time in the flowers (on average ca. 25 sec), followed by "*Euglossa* 1" (20 sec) and "*Euglossa* 2" (12 sec).

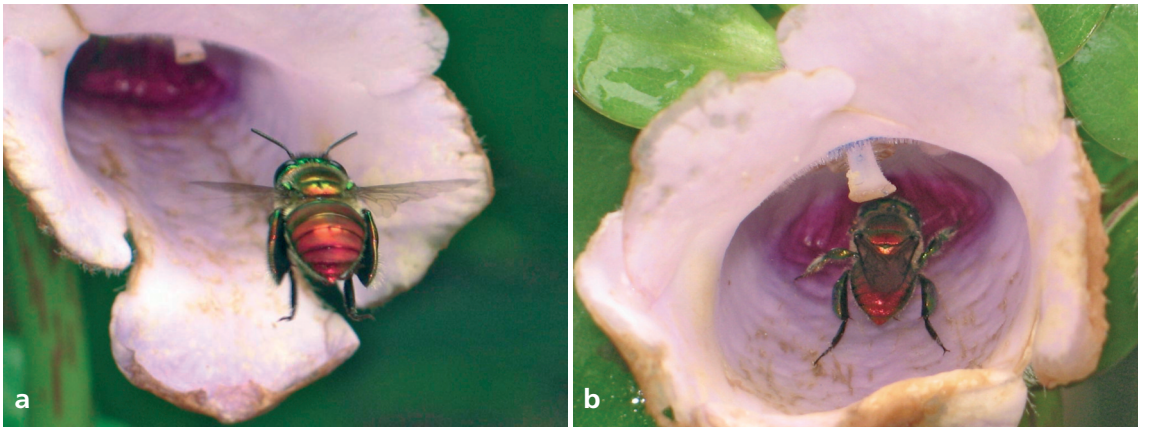

Fig. 6. *Euglossa* 1 (large-sized) approaching (**a**) and exploiting (**b**) a flower of *Gloxinia perennis.*

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Duration of upflight (back-loading). This was positively correlated with the collection time of the fragance: *Eulaema*: 5 s, *Euglossa* 1: 4 s, and *Euglossa* 2: 2 s.

Contact with anthers and pollen. Contact of the anther platform and stigma as well as pollen deposition was only observed in *Eulaema* (Fig. 5b, c). Both *Euglossa* species proved too small to get in contact with the pollen and stigma. The whitish pollen is mainly deposited on the bee's head. VOGEL (1966) reported pollen deposition in *Eulaema nigrita* on the first segment of the thorax (pronotum).

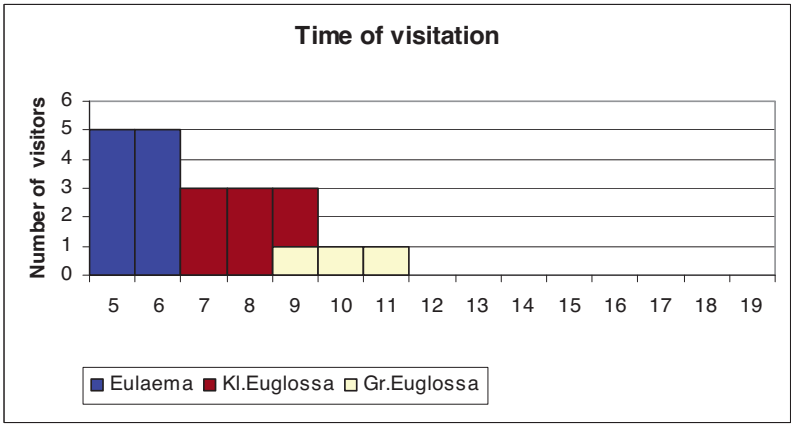

Fig. 7: Staggered flower visitation of *Eulaema meriana* (blue), *Euglossa* 2 (red) and *Euglossa* 1 (light).

Conclusions

The observations, although made in a very short observation period, clearly show that the fragrance provided by *Gloxinia perennis* is not addressed to a single species or genus of euglossines, but is attractive to several species. This complements hitherto existing observations which report exclusive visitation by *Eulaema*. However, both the large and the small *Euglossa* bees were found to be too small to contact the anthers and the stigma and can be excluded as effective pollinators. Only *Eulaema* bees have the approriate body size to effect pollination successfully, and correspondingly, the flowers of *Gloxinia perennis* are adapted to the large *Eulaema* bees, despite the fact that the fragrance is not specifically addressed to them. Moreover, the visitation of *Eulaema meriana* seems to be restricted to the early morning, long before the metallic *Euglossa* bees appear. This certainly results in a better harvest of fragrance. *Eulaema meriana* seems to follow a "first come, first served" strategy, and thus, it is the winner in the competition with other euglossine bees.

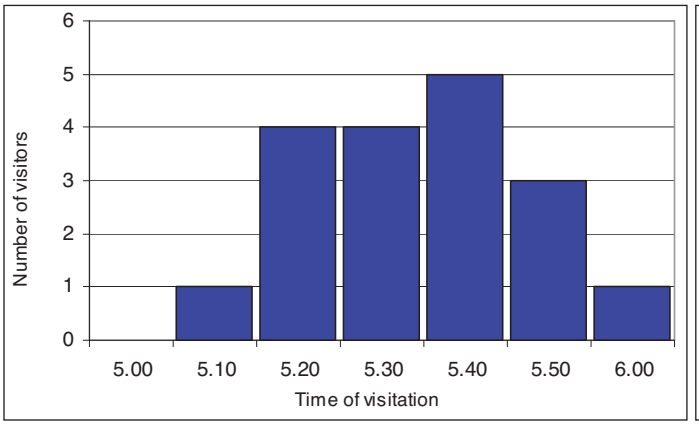

Fig. 8: *Eulaema meriana,* frequency of flower visitations.

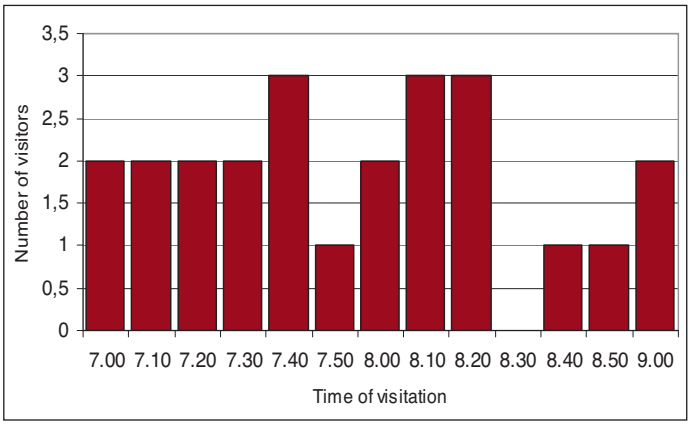

Fig. 9: *Euglossa* 2, frequency of flower visitations.

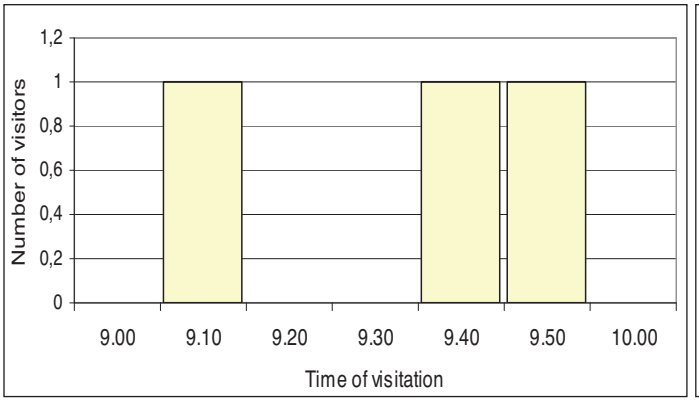

Fig. 10: *Euglossa* 1, frequency of flower visitations.

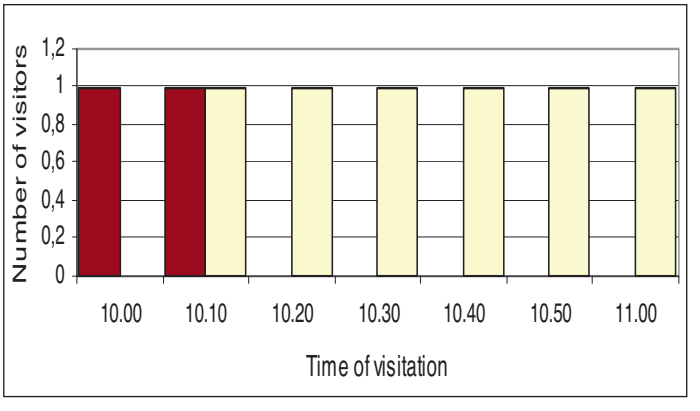

Fig. 11: *Euglossa* 1 and 2, frequency of flower visitations.

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At the moment, this is only a hypothesis. This must be tested by long-term investigations and complemented by field studies in other parts of the distribution area of *Gloxinia perennis*. Moreover, the remaining species of *Gloxinia* (*G. erinoides* – better known under its former name *Koellikeria erinoides* – and *G. xanthophylla*, formerly known as *Anodiscus xanthophyllus*) should be examined, as well as *Gloxiniopsis racemosa* (the former *Gloxinia racemosa*), which is extremely similar to *Gloxinia perennis* in habit and flower morphology. In addition, *Monopyle* species, which WIEHLER (1983) suspected to be andro-euglossophilous, also should be included in future investigations.

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