

# Reproductive biology and pollination of *Govenia utriculata*: A syrphid fly orchid pollinated through a pollen-deceptive mechanism

EMERSON R. PANSARIN

University of São Paulo, FFCLRP, Department of Biology, Av. Bandeirantes, 3900, 14040-901, Ribeirão Preto, SP, Brazil

## Abstract

The reproductive biology and pollination mechanisms of *Govenia utriculata* (Sw.) Lindl. were studied in a mesophytic semideciduous forest at Serra do Japi, south-eastern Brazil. The floral visitors and pollination mechanisms were recorded, and experimental pollinations were carried out to determine the breeding system of this species. Populations of *G. utriculata* growing at Serra do Japi are exclusively visited and pollinated by two species of hoverflies in the genus *Salpingogaster* (Diptera: Syrphidae) that are attracted by deceit to the flowers of this orchid species. The lip apex and the column base present small brownish and yellow to orange spots that mimic pollen clusters. *Govenia utriculata* is self-compatible, but pollinator dependent. Natural fruit set was low (10%), but similar to that of other non-obligatorily autogamous sympatric orchid species that occur at Serra do Japi and of other fly-pollinated orchid species pollinated through deceptive mechanisms.

*Keywords:* floral biology, *Govenia*, Orchidaceae, pollination, syrphid flies, Syrphidae.

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## Introduction

*Govenia* Lindl. (Epidendroideae, Goveniinae) is a neotropical and terrestrial genus with up to 15 species distributed from Florida to Argentina, which includes *Govenia utriculata* (Sw.) Lindl. Dressler (1993) suggests that bees pollinate species of this genus. However, according to Ackerman (1995), the pollinator and breeding systems of *Govenia* are not well understood. Based on floral characteristics, Garcia-Cruz and Sosa (2005) suggest that some Mexican species are pollinated by small to large bumblebees, but that *G. utriculata* seems to be autogamous, as is the case for many different genera of the Orchidaceae (van der Pijl & Dodson 1966; Catling & Catling 1991). Ramírez and Seres (1994) pointed out that, in Venezuela, both *G. utriculata* and *Govenia fasciata* Lindl. are pollinated by *Eulaema speciosa* Mocsary.

As reported for some species of *Govenia* (Dressler 1993; Ramírez & Seres 1994; Seres & Ramírez 1995; Garcia-Cruz & Sosa 2005), most species of Orchidaceae are pollinated by Hymenoptera (van der Pijl & Dodson 1966; Dressler 1981). Bees either exploit different rewards or are attracted

to orchid flowers by deceit (van der Pijl & Dodson 1966; Dressler 1981). Approximately one-third of all Orchidaceae seem to be deceptive (van der Pijl & Dodson 1966; Ackerman 1986; Nilsson 1992) and, according to Dressler (1993), there are 4800 deceptive generalized 'food flower' mimics among orchids. Food fraud is one way that non-rewarding orchids attract their pollinators (Dafni 1984; Ackerman 1986; Nilsson 1992). Although most food-deceptive orchids are pollinated by nectar-seeking insects (Dafni 1984; Ackerman 1986), according to Dressler (1993) and Ackerman (1986) some orchid species attract their pollinators through pollen deception. The hair cluster on the lip of species of the vanilloid genus *Pogonia* (Dressler 1993), North American *Cleistis* (Gregg 1989), *Isotria* (Mehrhoff 1983) and *Calypso* (Boyden 1982) simulates pollen clusters and attracts pollinators by deceit. In addition to Hymenoptera, other insects, such as butterflies, moths and flies, are attracted to orchid flowers by deceit (see van der Pijl & Dodson 1966 for a review). Pollination by flies has been reported for several unrelated orchid genera (van der Pijl & Dodson 1966). In Brazil, myophily has been reported in *Pleurothallis* (Borba & Semir 2001) and *Bulbophyllum* (Sazima 1978; Borba & Semir 1998), genera that present typical characteristics for fly pollination (van der Pijl & Dodson 1966; Dressler 1981,

Correspondence: Emerson R. Pansarin  
Email: epansarin@uol.com.br

1993; Christensen 1994). Within Orchidaceae, myophily (i.e. pollination by flies) is the second largest pollination syndrome because approximately 20 families of Diptera are known to be involved (Christensen 1994). In Orchidaceae, pollination by hoverflies (Diptera: Syrphidae) occurs in some unrelated groups and has been recorded in all subfamilies within the orchid family, except Vanilloideae (see Christensen 1994). According to Christensen (1994), species pollinated by flies present low specificity and are considered to have one of the most generalized pollination systems (van der Pijl & Dodson 1966; Faegri & van der Pijl 1979), but see Borba and Semir (1998, 2001).

According to Garcia-Cruz and Sosa (2005), Mexican species of *Govenia* are the only species to have received attention with respect to their phylogeny, taxonomy and some aspects of their floral biology. In fact, no information on floral biology is available for any of the South American species or for most of the Central American species (Garcia-Cruz & Sosa 2005). Based on records of their phenology, floral morphology, pollination mechanisms, compatibility system and natural fruit set, this paper reports on the floral biology and reproduction system of the pollen-deceptive pollinated orchid *G. utriculata*. The present work is the first record of pollination by hoverflies in Goveniinae. Although visitations (Pansarin 2000; Pansarin & Amaral 2006) and pollinaria removal (Singer & Cocucci 1999) by syrphid flies have previously been recorded in some Orchidaceae species in south-eastern Brazil, this is the first study to examine the pollination mechanism in this subtribe and to document pollination by hoverflies in a South American orchid.

## Materials and methods

### Study site

The pollination mechanisms and reproductive biology of *G. utriculata* were studied in a mesophytic semideciduous forest in the Serra do Japi district of Jundiaí (approximately 23°11'S, 46°52'W; 700–1300 m a.s.l.). In the Serra do Japi, the annual rainfall is approximately 1500 mm and the mean annual temperature is approximately 17.5°C (Pinto 1992). This region is mainly characterized by semideciduous mesophytic forests of medium altitude with occasional rocky outcrops (Leitão-Filho 1992).

### Plant and flower features

Fieldwork was carried out during two *G. utriculata* flowering seasons, from September to October 1998 and from October to December 2006. Data on the production of pseudobulbs, leaves and inflorescences, and on the features of flower anthesis and fruit dehiscence were recorded.

The morphological features of fresh and formalin-acetic acid-alcohol preserved flowers collected in the field ( $n = 30$ ) were recorded and drawn with the aid of an Olympus SZH10 stereomicroscope (Olympus, Rungis, France) equipped with a camera lucida. Measurements were made from drawings and directly from floral structures using alipers. The presence of nectaries was checked by dissecting the flowers. Fresh flowers were immersed in neutral red to localize osmophores (Dafni 1992). The plant voucher, Jundiaí, I. 2004, E.R. Pansarin & L. Mickeliunas 1112, was deposited at the Herbarium of the Universidade Estadual de Campinas.

### Pollination mechanism and pollinators

Data on pollinators, the pollination process and visitation frequencies to flowers of *G. utriculata* were collected by observing a group of 12 flowering plants (12 inflorescences) during the 2006 flowering period, from 16 to 21 October and from 3 to 8 November, and some pollinators were captured for later identification. The daily observation period was from 06.00 hours to 16.00 hours on sunny days, totaling 120 h. Previous observations (50 h) had been made during the 1998 flowering period (12 plants; 12 inflorescences), from 9 to 13 September. At the end of each observation day the flowers were tagged and examined the following morning at approximately 06.00 hours to detect possible nocturnal pollination. Insects were collected, identified and vouchers were deposited at the Museu de História Natural of the Universidade Estadual de Campinas.

### Compatibility system and natural fruit set

Experimental treatments to investigate the compatibility system of *G. utriculata* were carried out in the natural habitat during the 2006 flowering period. These treatments included manual self-pollinations and cross-pollinations and emasculations, with 30 flowers (eight plants; eight inflorescences) per treatment. Treatments were randomly applied to each inflorescence using flowers at their first day of anthesis. As a control, 37 flowers (four plants; four inflorescences) were left untouched. The fruit set under natural conditions (open pollination) of 149 flowers (12 plants; 12 inflorescences) was recorded when fruits were dehiscent.

## Results

### Phenology, plant and flower features

At Serra do Japi, *G. utriculata* occurs as a terrestrial plant and grows under the shade of trees or in the disturbed areas of forest margins. Between August and October, each young stem, a subterranean corm, grows one or two large

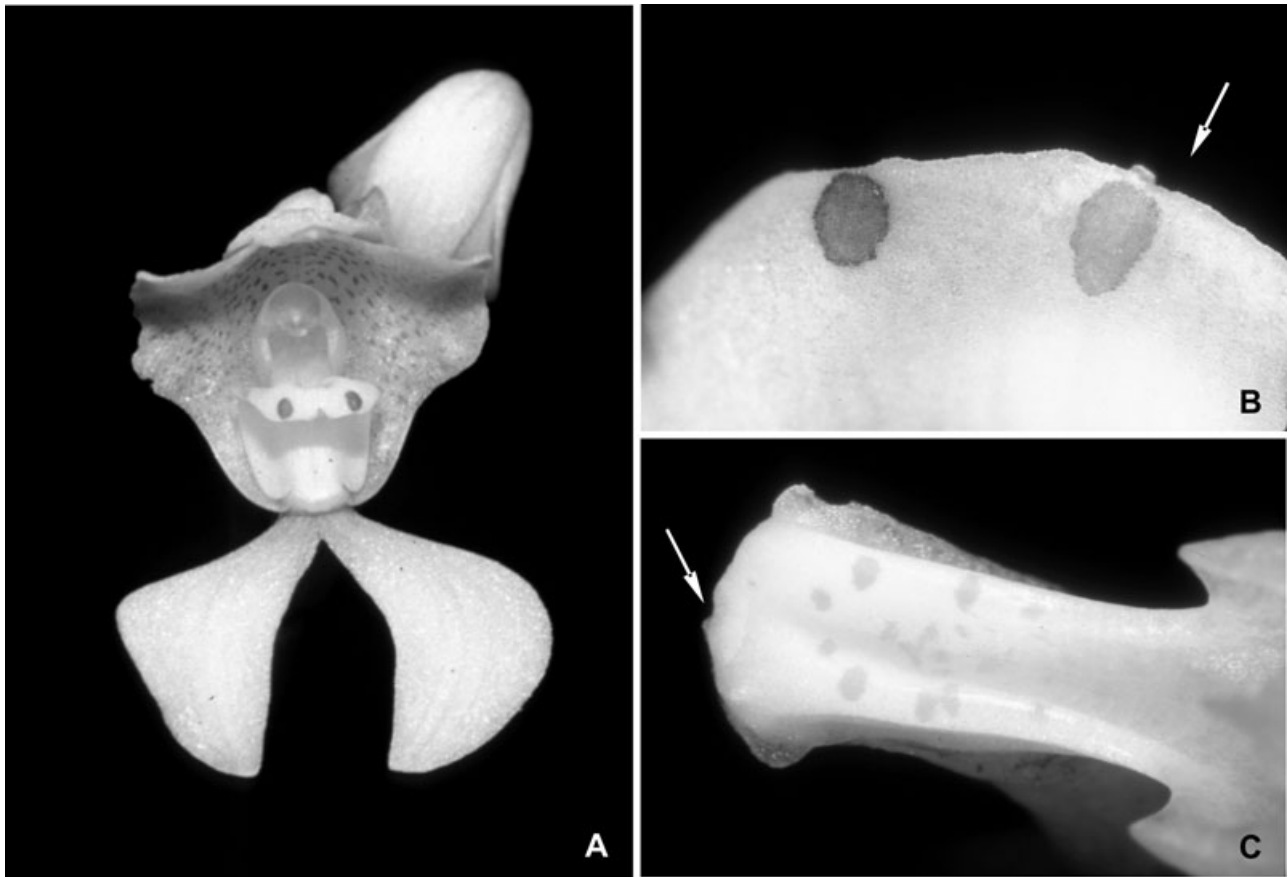


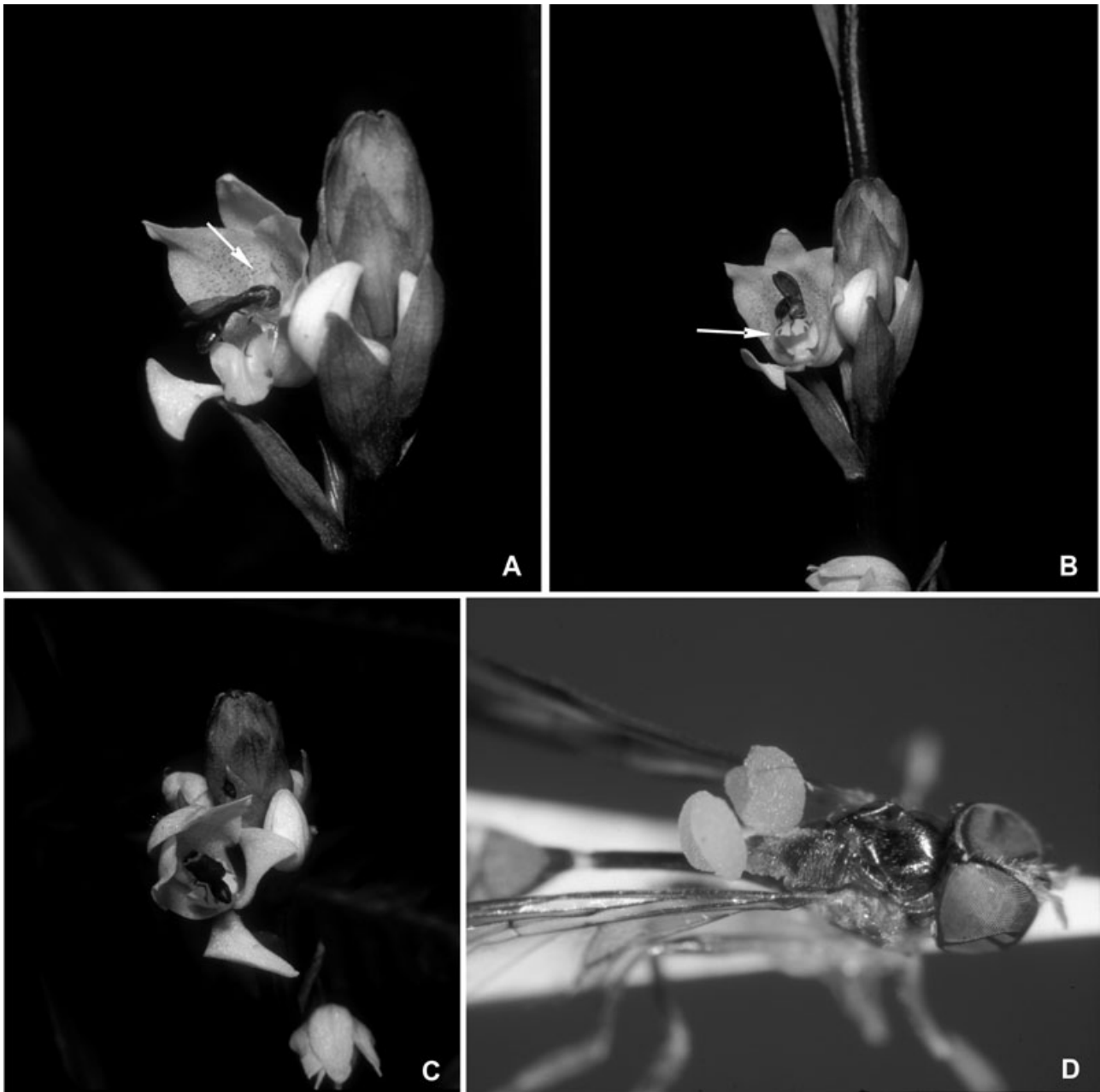
Fig. 1 *Govenia utriculata*. (A) Flower in frontal view, (B) lip apex (arrow) with alternating brown and orange spots, and (C) detail of the column base (arrow) showing the orange spots.

and plicate leaves. The lateral and scapose raceme produces up to 26 flowers opening in succession. Flowers are resupinate, showy, pale rose with a dorsal sepal and petals hooded over the column (Fig. 1a). The one-lobbed labelum measures approximately 10 mm × 7 mm, is broadly elliptic to oblong and convex, with a longitudinal and central slit. It is yellowish white or pale rose-yellowish with (approximately 0.5 mm) yellow and brown dots alternating on its rounded apex (Fig. 1b). The lip is attached (articulate) to the short column foot. The arched column (approximately 7–8 mm) is white, longitudinally sulcate, winged near the apex, with minute orange spots and a short foot at the base (Fig. 1c). The stigma is concave, transversely oval and measures approximately 2 mm in length. The pollinarium presents four hard, waxy and circular pollinia that are approximately 1 mm. Anthesis occurs in the morning and each flower lasts 7–8 days.

#### *Pollination mechanism and pollinators*

Flowers of *G. utriculata* were exclusively visited and pollinated by two species of flies from the genus

*Salpingogaster* (Diptera: Syrphidae). A total of 46 visits were recorded during the observation periods in 1998 and 2006. Visits occurred from 08.00 to 15.00 hours, but were more frequent from 10.00 to 13.00 hours. The flies hovered in front of the flower for 2–10 s before landing on the yellow and brown spots of the margin of the apex lip. Due to the weight of the fly the lip tips down. When the fly heads for the lip base that, as the labelum apex, has dark spots, it passes the equilibrium position and the lip recovers its original position, throwing the syrphid lengthwise onto the column (Fig. 2a). The dorsal thorax (scutum) of the fly is positioned below the viscidium (Fig. 2b). The fly has to struggle to pull itself out and as it does the pollinia sticks to its scutum (Fig. 2d). Once trapped, the syrphid holds the lip and forces it backwards (Fig. 2c). The struggle to escape can last up to 37 min, and no fly ever returns to the flower after a pollinarium is removed. The hoverflies recorded as pollinators of *G. utriculata* were frequently observed visiting cobloving species that offer pollen as a resource, such as species of *Piper* (Piperaceae), *Tripogandra* (Commelinaceae) and *Begonia* (Begoniaceae).



**Fig. 2** Pollination mechanism of *Govenia utriculata* by *Salpigogaster* spp. (A) Settled on the lip. Note the pollinarium deposited on its scutum (arrow). (B) Trapped between the lip and the column. Note the dark spots on the lip apex (arrow). (C) Disarticulating the lip to abandon the flower. (D) Detail of a hoverfly with a pollinarium on its dorsal thorax.

#### *Compatibility system and natural fruit set*

*Govenia utriculata* is self-compatible, but is dependent on a pollen vector for fruit set. Fruit set was 70% and 63.3% in self-pollinated and cross-pollinated flowers, respectively. No fruits developed after emasculations or in control (untouched) flowers. Under natural conditions, fruit set was low, with approximately 10% dehiscent fruits in the 2006 flowering period. Fruits were dehiscent 5 months

after pollination. The results of the experimental treatments are summarized in Table 1.

#### **Discussion**

Based on floral features such as diurnal anthesis, zygomorphy, the presence of nectar guides, a sweet fragrance and semi-open, shallow and white to yellow-colored

**Table 1** Total flower number and percentage of fruit set in each treatment of *Govenia utriculata* and fruit set in natural conditions (open pollination) at Serra do Japi

Treatments	Flower	Fruit set (%)
Self-pollination	30	70 (21)
Cross-pollination	30	63.3 (19)
Emasculation	30	(0)
Untouched flower (control)	37	(0)
Open pollination	149	10 (15)

Numbers in parentheses are the number of fruits formed.

flowers, several species of *Govenia* are considered to be pollinated by either small or large bumblebees (Garcia-Cruz & Sosa 2005), although Ramírez and Seres (1994) and Seres and Ramírez (1995) reported pollination by *Eulaema speciosa* for two species of *Govenia*, including *G. utriculata*, in Venezuela. However, in populations growing at Serra do Japi, *G. utriculata* is exclusively visited and pollinated by syrphid flies of the genus *Sappingogaster*, which are attracted to this orchid species by deceit. According to Waser *et al.* (1996), one of the limitations of several studies about specificity is that they survey only one population per plant species. In the majority of the studies that have included more than one population, variation in pollinator species has been observed (see Horvitz & Schemske 1990; Waser *et al.* 1996). Thus, as pointed out by Borba and Semir (2001), in widespread species, such as *G. utriculata*, studies in other regions should be interesting from an ecological view.

The pollination mechanism recorded here for *G. utriculata* is common in myophilous species within Orchidaceae (see van der Pijl & Dodson 1966; Chase 1985; Singer & Cocucci 1999; Borba & Semir 2001). Pollination by syrphid flies, as observed for *G. utriculata* at Serra do Japi, has already been reported in several orchid sub-families (see Christensen 1994 for a review). Some orchid species are pollinated by nectar-seeking syrphids (Knuth 1909; Gilbert 1958; Bernhardt & Burns-Balogh 1986). However, as reported here for *G. utriculata*, most orchids pollinated by hoverflies attract their pollinator by deceit (see Christensen 1994 for a review). The attraction of the pollinators and the pollination system of *G. utriculata* appears to be related to *Thelymitra*, in which some species attract pollinators from coblooming flowers by mimicking their stamens (Bernhardt & Burns-Balogh 1986; Dafni & Calder 1987; Burns-Balogh & Bernhard 1988).

Although little is known about the relationships between orchids and flies (Dressler 1981), myophily seems to be a generalized pollination system (van der Pijl & Dodson 1966; Faegri & van der Pijl 1979). Specificity

within myophilous species has only been recorded occasionally (see van der Pijl & Dodson 1966; Borba & Semir 1998, 2001). Although Diptera are the second most important group of orchid pollinators (van der Pijl & Dodson 1966; Christensen 1994), to date, fly-pollinated orchids have only been described in tropical orchids of the tribes Dendrobieae (subtribe Bulbophyllinae) and Epidendreae (subtribe Pleurothallidinae) (Christensen 1994; Borba & Semir 2001). Moreover, in nectarless species of the latter, the orchid-pollinator relationship has already been described as species specific (Borba & Semir 2001).

Plants of *G. utriculata* growing in the Serra do Japi are unable to reproduce through autonomous selfing and are completely dependent on pollinators to set fruits. Other studies have reported the occurrence of spontaneous self-pollination in Venezuelan populations of this specie (see Ramírez & Seres 1994; Garcia-Cruz & Sosa 2005). Moreover, our data show a significantly lower fruit set following manual self-pollination and cross-pollinations. A number of studies reveal that in widely distributed orchid species, such as *Stenorrhynchos lanceolatum* (Aubl.) Rich. ex Spreng., both autogamous and pollinator-dependent populations occur (Singer & Sazima 2000). The occurrence of autogamy in this case can evolve as a consequence under conditions of pollinator scarcity (Catling & Catling 1991). As reported in the present study for *G. utriculata* growing at Serra do Japi, orchids are usually considered self-compatible, and autogamy is mainly prevented by herkogamy and pollinator behavior (e.g. van der Pijl & Dodson 1966; Dressler 1981, 1993; Nilsson 1992) or pre-pollination mechanisms (e.g. van der Pijl & Dodson 1966; Adams & Goss 1976; Stoutamire 1978; Ackerman & Mesler 1979; Catling & Catling 1991; Singer & Cocucci 1999). These mechanical barriers are mainly associated with plants pollinated by insects that often remain on the flowers and inflorescences for a long time, promoting geitonogamy, as reported for some myophilous species (Christensen 1992; Pedersen 1995; Borba & Semir 1998; Singer & Cocucci 1999; Borba & Semir 2001). In plants of *G. utriculata* at Serra do Japi, self-pollination is prevented because the labelum tips the hoverflies out after pollinarium removal and these insects were never observed returning to the same inflorescence after abandoning a flower. According to Borba and Semir (1998), a similar mechanism to that of *G. utriculata* prevents self-pollination in species of the genus *Bulbophyllum* in south-eastern Brazil.

The natural fruit set of *G. utriculata* was low (10%), but this is similar to the fruit set of other sympatric and non-obligatorily autogamous reward-producing orchid species occurring at Serra do Japi (Pansarin 2000, 2003; Mickeliunas *et al.* 2006; Pansarin *et al.* 2006). In addition, *G. utriculata* shows a natural fruit set similar to that of other fly-pollinated orchid species that are pollinated

through deceptive mechanisms (e.g. Dafni & Calder 1987; Borba & Semir 1998, 2001).

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