

Chiropterophily in Sinningieae (Gesneriaceae): *Sinningia brasiliensis* and *Paliavana prasinata* are bat-pollinated, but *P. sericiflora* is not. Not yet?

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• **Background and Aims** Based on the bell shape and greenish colour of the flowers, bat-pollination was suggested for some Sinningieae species (Gesneriaceae). Actually, there are no reports on pollination biology and visitors for these species. This paper reports on pollination biology of *Sinningia brasiliensis*, *Paliavana prasinata* and *P. sericiflora* in south-eastern Brazil.

• **Methods** Flowers were observed *in situ* to determine phases of anthesis, colour patterns and scent intensity. Corolla measures were taken from fresh flowers. Nectar production and concentration were measured in flowers bagged at the pre-anthesis phases. Direct visual observations of visitors were made during the day and night, and photographs were taken to analyse their visiting behaviour.

• **Key Results** Some floral features of the three species fit the bat-pollination syndrome: large, robust and gullet-shaped corollas, colour patterns and large amount of nectar. However, other floral features—such as onset of anthesis, nectar attributes and odour intensity—differ among the species. Nectar volume and total sugar production increased significantly at midnight in *S. brasiliensis* and *P. prasinata*, but in *P. sericiflora* there were no significant differences in the total nectar and sugar production during anthesis. Scent intensity is much higher in *S. brasiliensis* and *P. prasinata* than *P. sericiflora*. Flowers of *S. brasiliensis* and *P. prasinata*, whose features fit the chiropterophilous syndrome, are pollinated by glossophagine bat species. *Paliavana sericiflora*, on the other hand, presents floral features intermediate between bat and hummingbird syndromes, but is visited and pollinated only by hummingbirds.

• **Conclusions** These data strengthen the statement that the bat syndrome in Sinningieae originated independently in *Sinningia brasiliensis* and in *Paliavana* species. *Paliavana sericiflora* may be another example of a plant 'in transition' from the hummingbird to the bat pollination, but a reversion in the direction of bat to hummingbird might not be excluded. It is also possible that this is a case of speciation on both bat and hummingbird pollination. Studies on *Paliavana* sister species may provide insights about origins and the evolutionary directions of the pollination systems of these species.

Key words: Gesneriaceae, *Sinningia brasiliensis*, *Paliavana prasinata*, *P. sericiflora*, floral biology, pollination, chiropterophily, ornithophily, south-eastern Brazil.

INTRODUCTION

Sinningieae (Gesneriaceae) is a neotropical monophyletic tribe comprising three genera: *Sinningia* Nees, *Vanhouttea* Lemaire and *Paliavana* Vandelli (Smith *et al.*, 1997). The majority of the species belong to the tuberous genus *Sinningia*, which is distributed throughout the Neotropics, except in the Caribbean area (Chautems and Weber, 1999). *Vanhouttea* and *Paliavana* have a narrow distribution occurring mostly in south-eastern Brazil (A. Chautems, Conservatoire et Jardin botaniques de la ville de Geneve, Switzerland, pers. comm.). Based on floral shape, colour, nectar sugar composition and scent, bees and hummingbirds were inferred as the putative pollinators for 93 % of the Sinningieae species by Perret *et al.* (2003). Most *Sinningia* species fit the ornithophilous syndrome as do those of *Vanhouttea* (I. SanMartin-Gajardo and M. Sazima, pers. obs.), whereas *Paliavana* species fit either the large bee or bat syndromes (Wiehler, 1983).

Based on the bell shape and greenish colour of the flowers, Vogel (1969) suggested that *Sinningia brasiliensis* (Regel and Schmidt) Wiehler and Chautems, *Paliavana*

prasinata (Ker-Gawler) Benth. and *P. sericiflora* Benth. were bat-pollinated. This is also supported by the low sucrose proportion found in *P. prasinata* and *S. brasiliensis* (Perret *et al.*, 2001), which is similar to that found in other Neotropical bat flowers (Baker *et al.*, 1998). However, there are no reports on pollination biology and visitors for chiropterophilous species within the tribe Sinningieae.

This paper reports on floral biology and pollination of *S. brasiliensis*, *P. prasinata* and *P. sericiflora*. The purposes were two-fold: (1) to confirm pollination by bats for the two former species; and (2) to discuss the intermediate floral features (between hummingbird/bat syndromes) of *P. sericiflora* and its pollination by hummingbirds.

MATERIALS AND METHODS

Fieldwork on *S. brasiliensis* and *P. prasinata* was carried out at the rupicolous gardens of the Museu de Biologia Mello Leitão (MBML) and at the Estação Biológica Santa Lúcia (EBSL), both in Santa Tereza (19°57'S and 40°31'W, 700 m a.s.l.), Espírito Santo, Brazil. The annual average temperature is 20°C and annual rainfall reaches 1327 mm, with a wet season from November to March

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(Thomaz and Monteiro, 1997). The EBSL area is covered by montane rainforest (Oliveira-Filho and Fontes, 2000), where *S. brasiliensis* and *P. prasinata* individuals occur on rocky outcrops. The pollination biology of *S. brasiliensis* was studied from 14 to 20 Jan. 2002 and of *P. prasinata* from 13 to 16 Jul. 2000 (at the EBSL) and from 18 to 22 Jun. 2001 (at the MBML). *Paliavana sericiflora* was studied at São Tomé das Letras (21°50'S and 44°52'W, 1300 m a.s.l.) and at Serra do Caraça (20°05'S and 43°28'W, 1200 m a.s.l.), both in Minas Gerais, Brazil. The mean annual temperature is about 18°C (Nimer, 1972) and annual rainfall is up to 1600 mm with a defined wet season from October to April. *Paliavana sericiflora* occurs on rocky outcrops of the typical montane fields that are called 'campos rupestres' a short grass savana intermixed with other rupicolous communities (Giulietti and Pirani, 1988). The pollination biology of *P. sericiflora* was studied from 26 to 31 Mar. 2001 (São Tomé das Letras) and from 26 to 30 Jun. 2002 (Serra do Caraça).

Flowers were observed *in situ* to determine phases of anthesis, colour (following Kornerup and Wanscher, 1963) and scent intensity (30 flowers of each species). Pollen viability was estimated by cytoplasmic staining, using the aceto-carmin technique (Radford *et al.*, 1974). Stigmatic receptivity was tested using the H₂O₂ catalase activity method (Zeisler, 1938). Effective corolla length (cf. Wolf *et al.*, 1976) and diameter of corolla opening were taken from fresh flowers sampled from different plants. Plant vouchers are deposited at the Herbarium of the Universidade Estadual de Campinas (UEC 113858 and UEC 111253) and Museu de Biologia Mello Leitão (MBML10183).

Nectar production was measured in flowers bagged at the pre-anthesis phase (number of flowers sampled per individual; Table 1). Two variables were measured, volume of nectar using a graduated microlitre syringe (Hamilton, NV, USA), and sugar concentration (percentage sucrose, w/w) with a pocket refractometer (Atago HSR 500, Japan). The amount of sugar was expressed in milligrams and calculated following Bolten *et al.* (1979). Flowers were bagged for 24 h to measure the accumulated nectar (flowers in which nectar dripped out were excluded). Total nectar volume, nectar sugar concentration and total sugar production was compared among different species by one-way ANOVA test and unequal *n* HSD *post hoc* test at the 0.05 significance level.

In another group of bagged flowers, all nectar was removed from the same flower repeatedly, at 6-h intervals for *Paliavana* species and at 8-h intervals for *S. brasiliensis*, starting at 1800 h on the first day of anthesis until corolla abscission. Care was taken to avoid damage to the nectaries and other flower parts. The mean of nectar volume, nectar sugar concentration and total sugar produced per time interval by *S. brasiliensis* (*n* = 6), *P. prasinata* (*n* = 7) and *P. sericiflora* (*n* = 9) flowers were compared by Kruskal-Wallis ANOVA test and Dunn *post hoc* test at the 0.05 significance level.

Direct visual observations of bat visitors were made by sky- or moonlight and photographs were taken to analyse their visiting behaviour. Observations on *S. brasiliensis*

TABLE 1. Nectar production measured from flowers bagged during the first 24 h of anthesis

Species	Flowers/ individuals (<i>n</i>)	Nectar volume (μ L)	Nectar concentration (% w/w)	Amount of sugar (mg)
<i>Sinningia brasiliensis</i>	12/10	85 \pm 42	17.5 \pm 2.6	15 \pm 7.1
<i>Paliavana prasinata</i>	22/8	82 \pm 38	14.3 \pm 3.6	12.1 \pm 6.6
<i>P. sericiflora</i>	15/15	87 \pm 42	23.2 \pm 2.0	21.8 \pm 10.1

(15 plants) were made during 4 d from 1700 to 0330 h (totalling 22 h), and on *P. prasinata* (10 plants) during 3 d from 1730 to 0700 h (totalling 30 h). No focal daytime records were made on *S. brasiliensis* and *P. prasinata* as the pollen was removed during the night (10 and 20 flowers checked, respectively). On *P. sericiflora*, observations were made from 1730 to 0030 h (totalling 39 h), during 3 d in São Tomé das Letras and 4 d in Serra do Caraça. In addition, to detect bat visits, 15 flowers of *P. sericiflora* in the male phase were marked and examined in the early morning for nightly pollen removal. Hummingbird visits to *P. sericiflora* were observed from 0600 to 1800 h, totalling 30 h.

RESULTS AND DISCUSSION

Plant habit and floral features

Sinningia brasiliensis is an annual herb measuring 0.5–1.5 m tall, and *Paliavana prasinata* and *P. sericiflora* are perennial shrubs 1–3 m tall. The flowering periods of the study populations occurred once a year and lasted from December to February in *S. brasiliensis*, April to August in *P. prasinata*, and February to May in *P. sericiflora*, characterizing an annual phenological pattern as defined by Newstrom *et al.* (1994).

Sinningia brasiliensis has terminal inflorescences with axillary, long-stalked (35–70 mm) flowers. The long stalk ensures that flowers are positioned outside the foliage, which is typical of bat flowers (Faegri and van der Pijl, 1980). *Sinningia brasiliensis* flowers are delicate, of the gullet-type (cf. Faegri and van der Pijl, 1980), with a hooded corolla (galea) formed by the fusion and expansion of two dorsal corolla lobes. Corolla mean length is 33 mm (s.d. = 1.9, *n* = 20) and the mean diameter of the corolla mouth is 18 mm (s.d. = 1.6, *n* = 20). The flowers are green coloured with violet-brown markings (Fig. 1A), which are quite variable among individuals. In both *Paliavana* species the flowers are robust, axillary, relatively short stalked (15–18 mm), but very accessible to visitors, and disposed in two-flowered cymes. The flowers of *P. prasinata* are of the gullet-type (cf. Faegri and van der Pijl, 1980), green in colour (Fig. 1B) with violet brown dots on the outside. Mean corolla length is 33 mm (s.d. = 2.3, *n* = 28) and its mean diameter is 17 mm (s.d. = 1.7, *n* = 30). The corolla shape and size (length and width of corolla opening) of *S. brasiliensis* and *P. prasinata* fit well to the bat visitor inserting its face or head in search of nectar, as predicted by Vogel (1969), and conform to the so-called 'glossophagine flowers' (von Helversen, 1993).

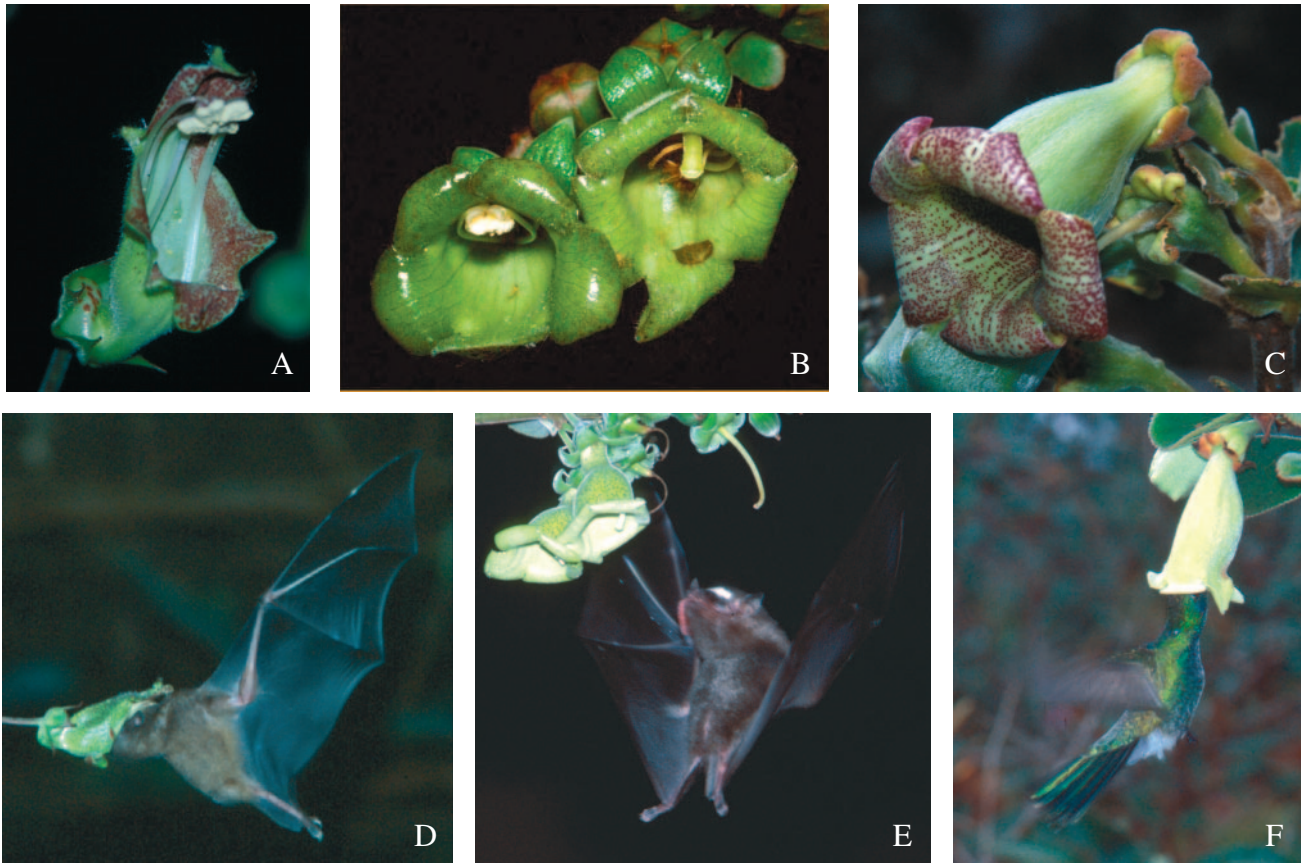


FIG. 1. (A) *Sinningia brasiliensis* flower in the first night of anthesis (male phase) showing the characteristic anther disposition. (B) Frontal view of *Paliavana prasinata* flowers; male phase with full anthers (left) and female phase with extended style (right). (C) Gullet-type flower of *P. sericiflora*; note the reddish calyx. (D) *Glossophaga soricina* on flower of *Sinningia brasiliensis*, its snout deep into the corolla. (E) *Paliavana prasinata* visited by *Anoura caudifer*; note the whitish pollen adhered on bat's forehead. (F) The hummingbird *Colibri serrirostris* visiting the tubular-type flower of *Paliavana sericiflora*.

The flowers of *S. brasiliensis* and *P. prasinata* open at sunset (between 1730 and 1800 h) and often last two nights, or occasionally three nights—a short anthesis period not yet reported for *Sinningieae* species (SanMartin-Gajardo and Sazima, 2004), but known for some bat-pollinated species of diverse families (Sazima *et al.*, 1989; Machado *et al.*, 1998; Sazima *et al.*, 1999), albeit one-night flowering is a more common pattern (Faegri and van der Pijl, 1980; Dobat and Peikert-Holle, 1985). During the first night (male phase), the anthers are situated at the upper rim of the corolla opening (Fig. 1A and B), the yellow-whitish pollen is available and its viability is approx. 90%. At this time the stigma is hidden behind the anthers and is not receptive. In the second and third night (female phase), the anthers are situated on the lower surface of the corolla and the now receptive stigma is exhibited (Fig. 1B). In general lines, placement and disposition of the reproductive organs follow the pattern known for *Gesneriaceae* (Wiehler, 1983).

Paliavana sericiflora flowers are of the gullet-type and greenish (Fig. 1C), or tubular and yellowish (Fig. 1F), but both types have violet brown dots inside the corolla, and the calyx is reddish and persistent. The corolla has a mean length of 43 mm (range 33–50 mm, s.d. = 3.6, $n = 47$) and a mean diameter of 16 mm (range 11–22 mm, s.d. = 2.9, $n = 47$), but most of the flowers are close to the average,

indicating that they are transition forms. Some of the floral features such as gullet-type, width of the corolla opening, shape and colour are typical of the chiropterophilous syndrome (Vogel, 1969; Faegri and van der Pijl, 1980), whereas other features such as the reddish calyx and the long, somewhat tubular corolla, may be related to pollination by hummingbirds (Grant and Grant, 1968; Faegri and van der Pijl, 1980). In addition, *P. sericiflora* flowers open irregularly during the day or night, but crepuscular anthesis is rare. So far as is known, flower opening at no set time is not mentioned for other *Gesneriaceae* (e.g. Wiehler, 1983; Steiner, 1985), a feature which may support the proposed intermediate situation of this species between syndromes. Anthesis sequence in this species, as well as pollen and stigma features, is similar to that found in former species, but each reproductive phase, lasts 3–4 d. A long anthesis period, as in *P. sericiflora*, is more common in melittophilous (SanMartin-Gajardo and Sazima, 2004) and some ornithophilous (I. SanMartin-Gajardo and M. Sazima, pers. obs.) species of the tribe *Sinningieae*.

Nectar features

Nectar secretion is continuous in the flowers of the species studied, starting at pre-anthesis and stopping after

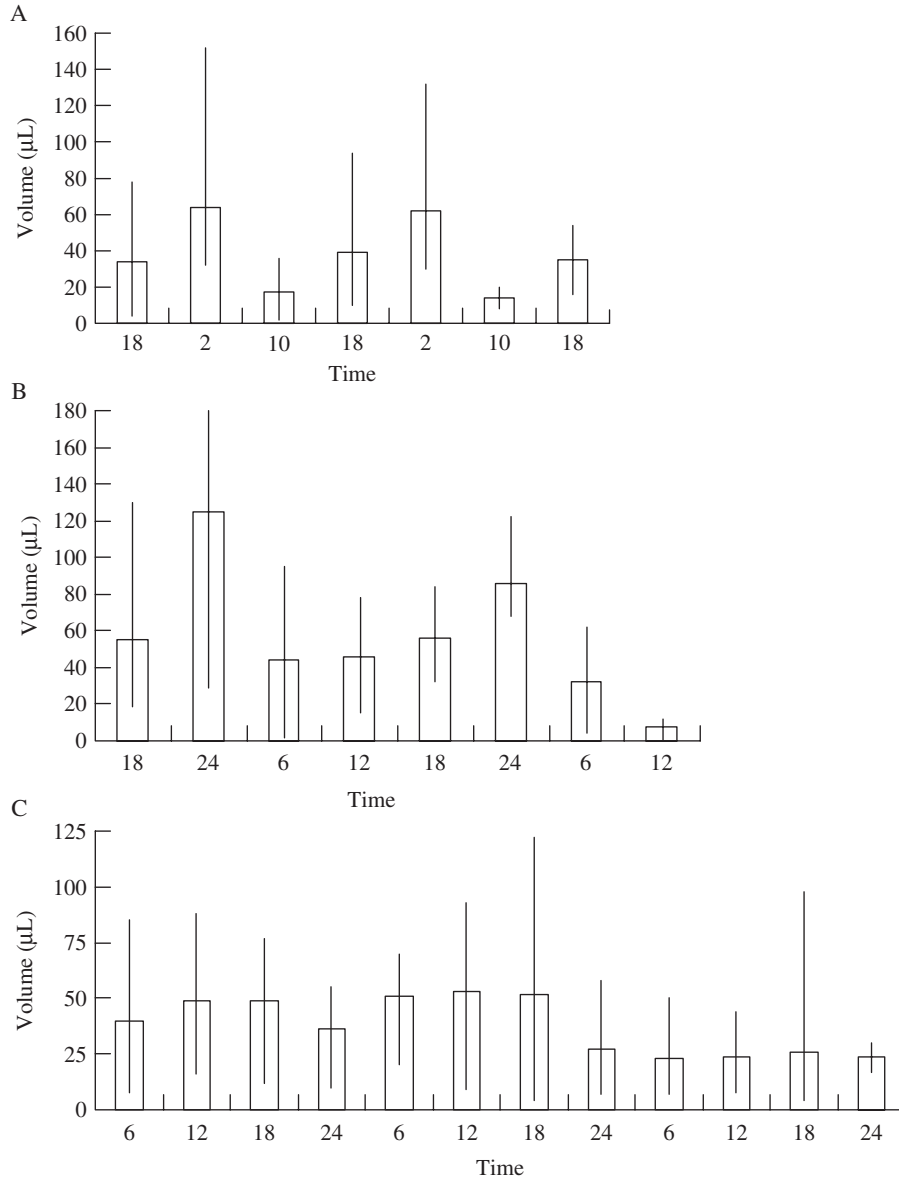


FIG. 2. Nectar volume produced by *S. brasiliensis* (A), *Paliavana prasinata* (B) and *P. sericiflora* (C) throughout anthesis. The columns represent the average and the vertical lines indicate the maximum and minimum ranges.

corolla fall. The average nectar volume accumulated during 24 h is high and similar in these species (Table 1), and also to the data reported by Perret *et al.* (2001) for *P. prasinata* and *S. brasiliensis* (mean = 88.9 µL). A large quantity of nectar, as occurs in the species studied, is a common attribute for bat flowers (Faegri and van der Pijl, 1980). Nectar concentration differs significantly among species (ANOVA, $df = 2, F = 40.5, P = 0.000$), and the amount of sugar differs significantly between *P. sericiflora* and the two other species (ANOVA, $df = 2, F = 6.7, P = 0.003$). The mean nectar concentrations in *S. brasiliensis* (17.5 %) and *P. prasinata* (14.3 %) are lower than in *P. sericiflora* (23.2 %; Table 1), but these values are similar to the range 5–29 % (often 15–17 %) found in 33 bat-pollinated flowers of the Neotropics according to von Helversen (1993). However, the mean

nectar concentration of *P. sericiflora* is also similar to the values of ornithophilous Gesneriaceae species, e.g. *Columnnea glabra* Oerst. (about 25–30 %) (Corbet and Willmer, 1981) and *Sinningia* species (22–25 %) (I. SanMartin-Gajardo and M. Sazima, pers. obs.).

The variation in nectar volume within each time interval throughout the flower lifetime was significantly different in *S. brasiliensis* (Kruskal–Wallis ANOVA, $H_{(2,62)} = 8.5; P = 0.01$), as well as in *P. prasinata* (Kruskal–Wallis ANOVA test, $H_{(3,56)} = 18.7; P = 0.0003$). Both species increased nectar volume significantly at 0200 h and 2400 h, respectively (Dunn test; $P < 0.05$) (Fig. 2A and B). This pattern of nectar production of *S. brasiliensis* and *P. prasinata* is similar to other bat-pollinated species (Buzato *et al.*, 1994; Sazima *et al.*, 1994; Slauson, 2000;

Petterson and Knudsen, 2001). In contrast to the former species, the nectar production in *P. sericiflora* shows no significant differences between periods of the day or night (Fig. 2C). High nectar volume produced by *P. sericiflora* and also sugar concentration (although 23 % is in the upper range of bat-pollinated species) fits well on the chiropterophilous syndrome, but production with no significant differences between periods is not common for bat-pollinated flowers (Faegri and van der Pijl, 1980; Dobat and Peikert-Holle, 1985; von Helversen, 1993).

Floral scents

The flowers of *S. brasiliensis* and *P. prasinata* exhale a strong fruity-sharp and very unpleasant smell. Scent production starts at sunset (approx. 1800 h), decreases progressively during the night, and ceases early in the morning. In contrast, flowers of *P. sericiflora* have a fruit-fermenting odour which is almost imperceptible throughout anthesis. It is probable that the scent intensity in *P. sericiflora* flowers is not strong enough to attract bats, which are able to detect and localize a food source guided only by the scent (von Helversen *et al.*, 2000), although other senses of glossophagine bats, like echolocation, are expected to be used to find flowers (von Helversen, 1993; von Helversen and von Helversen, 1999).

Visitors

Anoura caudifer (E. Geoffroy) was the only bat visitor recorded on *S. brasiliensis* flowers (Fig. 1D). This bat species and also *Glossophaga soricina* (Pallas) were recorded visiting the flowers of *P. prasinata* (Fig. 1E). These phyllostomid long-tongued bats are the major pollinators of bat-pollinated flower assemblages in the Atlantic rain forest (Sazima *et al.*, 1999). The bats arrived at the flowering plants of *S. brasiliensis* and *P. prasinata* at dusk (1830 h), and visits ceased at 0300 h in *S. brasiliensis*, and at dawn (0530 h) in *P. prasinata*. Before the first visit to a given flower, the bats made a pass close to the flower, probably assessing its condition (see Sazima *et al.*, 1999). The visits in both species occurred at regular intervals of 1–2 h in *S. brasiliensis* (frequency = 0.7 visits h⁻¹) and 10–20 min in *P. prasinata* (frequency = 3.7 visits h⁻¹). However, the intervals of visits decreased by half in the period from 2100 to 0100 h. The increase in visits at this time coincides with the increase of nectar production. This fact supports the idea of Zimmerman (1988), that the rate of nectar production will have significant effects on the behaviour of pollinators. Considering the optimal foraging theory of Pyke *et al.* (1977), it is possible that the nectar available to pollinators at a certain period may influence how often visits are made to the plants (see Rathcke, 1991). During their short hovering visits, the bats touched the flower's reproductive organs mostly with the forehead (Fig. 1D and E) and occasionally with the chin, where the pollen is placed in small patches. Selective pollen loading is known for several plants pollinated by the flower-specializing glossophagine bats (Vogel, 1969; von Helversen, 1993; Sazima *et al.*, 1999). Visits at regular intervals suggest trapliner

behaviour, which is commonly suspected in these bats (Heithaus, 1982; Lemke, 1984). They visited flowers of different individuals, a behaviour which favours cross-pollination and gene flow between adjacent populations (see Webb and Bawa, 1983). Hummingbirds visited flowers of both species, mainly in the early morning and late afternoon, but no contact with reproductive organs occurred.

Three species of hummingbirds were recorded on the flowers of *P. sericiflora*: the white-vented violetear, *Colibri serrirostris* (Vieillot), the stripe-breasted starthroat, *Heliomaster squamosus* (Temminck) and the hyacinth visorbearer, *Augastes scutatus* (Grantsau). The hummingbirds *C. serrirostris* and *A. scutatus* are common in the area and have been recorded visiting different flowering plants in the campos rupestres in Minas Gerais (Sazima, 1977; Sazima and Sazima, 1990; Vasconcelos and Lombardi, 2001). But, as far as is known, this is the first record of *Heliomaster squamosus* in this area. *Colibri serrirostris* was the most frequent visitor (1.6 visit h⁻¹) to *P. sericiflora* (Fig. 1F) and visits occurred throughout the day, whereas *H. squamosus* was a sporadic visitor (0.12 visit h⁻¹) with visits occurring at the beginning and the end of the day. During their visits, the birds touched the flower's reproductive organs with the upper forehead. *Colibri serrirostris* visited most of the individuals of the population in a sequence, at intervals of 20–30 min, and sometimes 70 min, characteristic of trapliner behaviour (Feinsinger and Colwell, 1978). This behaviour was also reported for *C. serrirostris* when visiting *P. sericiflora* in Serra do Caraça (Vasconcelos and Lombardi, 2001). *Augastes scutatus* visited the flowers of *P. sericiflora* by taking nectar through small holes in the corolla base, again as reported by Vasconcelos and Lombardi (2001). No bats were recorded visiting flowers of this species from 1730 to 0030 h, and no pollen removal occurred after this observation period.

The records on floral biology and pollination in *S. brasiliensis* and *P. prasinata* confirm the bat syndrome proposed by Vogel (1969) for these species, and strengthen Vogel's statement that the bat syndrome originated independently in *Sinningia brasiliensis* and in the *Paliavana* species, which was recently confirmed by the results of molecular systematics by Perret *et al.* (2003).

Although *P. sericiflora* flowers have intermediate characteristics between bird and bat syndromes this species is visited and pollinated only by hummingbirds. Intermediate pollination systems seem to be a relatively frequent event during the evolution of flowering plants, e.g. *Siphocampylus sulfureus* (Lobeliaceae) (Sazima *et al.*, 1994), *Abutilon* species (Malvaceae) (Buzato *et al.*, 1994) and species of *Burmeistera* (Campanulaceae) (Muchhala, 2003); however, these species differ from *P. sericiflora* in that they are pollinated by both nocturnal and diurnal visitors. The features of *P. sericiflora* flowers such as greenish colour with violet brown dots, wide opening and gullet shape, and large amount of nectar fit well in the chiropterophilous syndrome, but some characters such as crepuscular anthesis and strong unpleasant scent are lacking. The last feature seems to be decisive to attract bats (Tschapka and Dressler, 2002), a suggestion supported by Sazima *et al.* (1994) and Buzato *et al.* (1994), and might explain the absence of bats on

flowers of *P. sericiflora*. It is possible that *P. sericiflora* is another example of a plant 'in transition' (see Sazima *et al.*, 1994; Buzato *et al.*, 1994) from hummingbird to bat pollination syndromes a suggestion supported by the high number of hummingbird-pollinated species in the tribe Sinningieae as inferred by Perret *et al.* (2003). Another supposed bat-pollinated species in Sinningieae is *P. werdermannii* Mansf., the sister-species of *P. sericiflora* as proposed in the molecular phylogeny by Perret *et al.* (2003). In this case, both species may have ancestral features of the bat syndrome. Taking this assumption into account, reversion to hummingbird pollination might not be excluded for *P. sericiflora*. However, it is also possible that these species are cases of speciation on both bat and hummingbird pollination, and that such generalizations represent an evolutionary endpoint as argued by Muchhala (2003) for *Burmeistera* species. It is probable that field records about pollination of *P. werdermannii* should allow more inferences about origins and evolutionary directions of the pollination systems of these species.

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