

Nectar by day and night: *Siphocampylus sulfureus* (*Lobeliaceae*) pollinated by hummingbirds and bats¹

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Abstract: Most species of the neotropical genus *Siphocampylus* are believed to be bird-pollinated. The pollination biology of *Siphocampylus sulfureus* was studied in a montane region in SE Brazil. This species has features intermediate between ornithophilous and chiropterophilous syndromes: it presents a striking combination of yellowish flowers with strong odour (chiropterophilous features), and diurnal anthesis and sucrose-dominated nectar (ornithophilous features). Major pollinators were hummingbirds by day, and a phyllostomid bat by night. *Siphocampylus sulfureus* may be viewed as a recent derivate from the presumed ornithophilous stock within sect. *Macrosiphon*, and thus benefits from the activity of both diurnal and nocturnal vertebrate pollinators.

The genus *Siphocampylus* of the *Lobeliaceae* occurs in Central and South America and comprises about 200 species (WIMMER 1957; VOGEL 1969 a, b). The attractive, tubular flowers of *Siphocampylus* display various shades of red, red and yellow, orange, and less often yellow to greenish colour (WIMMER 1957). Data on pollination biology and/or flower visitors are scarce (e.g., SNOW & SNOW 1980, SNOW & TEIXEIRA 1982, GALETTO & al. 1993) and mostly inferred, *Siphocampylus* being regarded as a predominantly ornithophilous genus (WIMMER 1957; VOGEL 1969 a, b). About 170 species (85%) are believed to be bird-pollinated (Fig. 1 a), and the remainder is supposed to be bat-pollinated (VOGEL 1969 a, b). From the about 30 supposedly chiropterophilous species only four have been observed in the field, and in these the pollinator was inferred from floral syndromes (VOGEL 1969 a, b; DOBAT & PEIKERT-HOLLE 1985; see also Figs. 1 b and 2 c).

Siphocampylus sulfureus E. WIMM. was recently recorded as another presumably bat-pollinated species based on its floral syndrome (see appendix in DOBAT & PEIKERT-HOLLE 1985), although the very low sucrose/hexose ratio in its nectar may be regarded as a characteristic of flowers pollinated by hummingbirds (GOTTSBERGER & al. 1984, BAKER & BAKER 1990). In the present paper we report field

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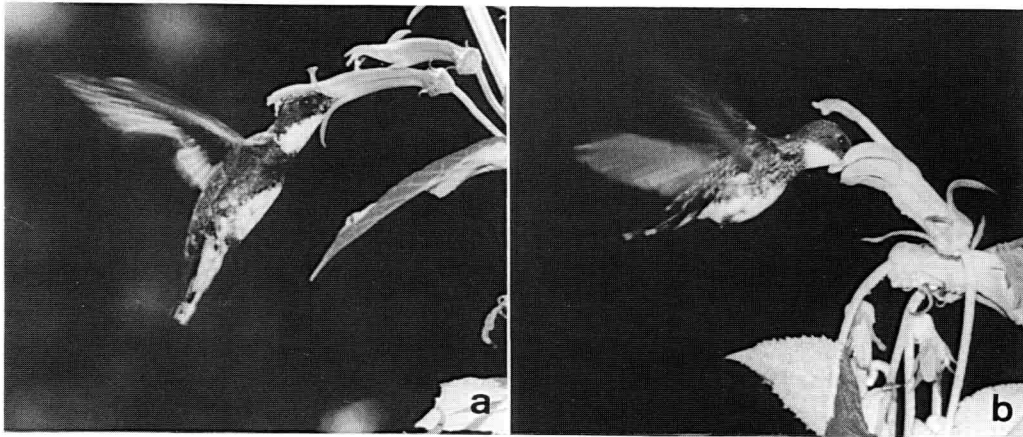


Fig. 1. An ornithophilous and a chiropterophilous species of *Siphocampylus*. *a* The White-throated Hummingbird, *Leucochloris albicollis* visiting the bird-pollinated flower of *S. cf. betulaefolius* (note fitting between bird head and flower corolla). *b* The same species of hummingbird thieving nectar from the bat-pollinated flower of *S. umbellatus*

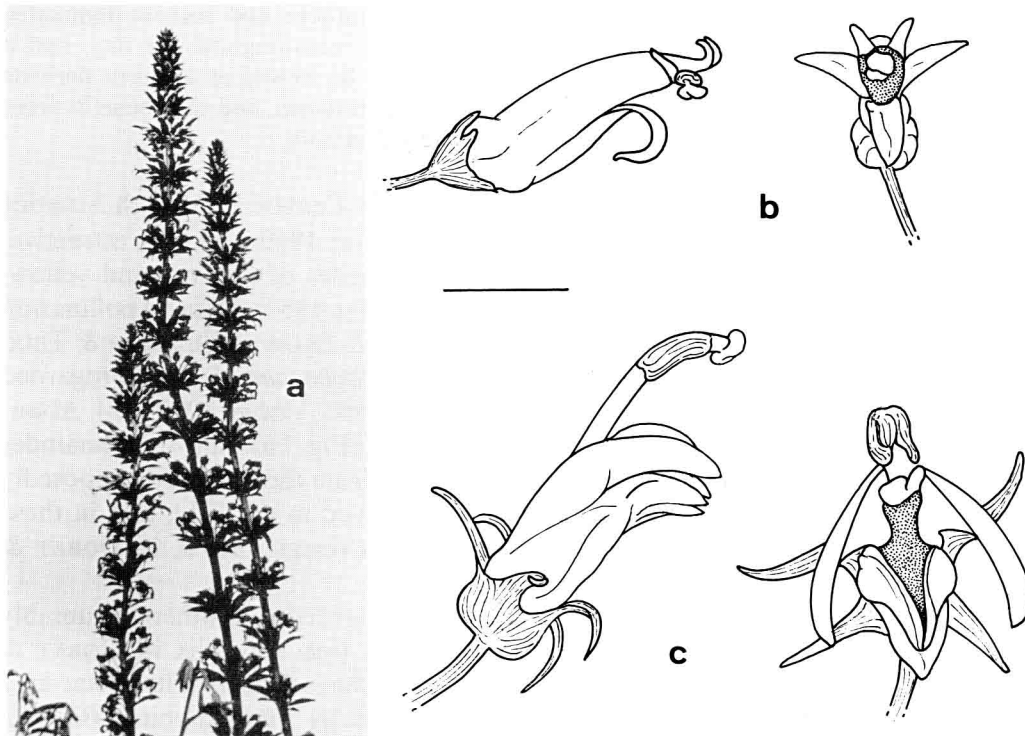


Fig. 2. Two species of *Siphocampylus* pollinated by bats. *a* Flowering and fruiting plants of *S. sulfureus* (note high fruit set below the flowering whorls). *b* Lateral and frontal views of *S. sulfureus* (sect. *Macrosiphon*). *c* Idem for *S. umbellatus* (sect. *Brachysiphon*). Bar: 20 mm

observations on the pollination of *S. sulfureus* and *S. umbellatus* (HBK.) G. DON in SE Brazil and discuss ornithophily and chiropterophily in this genus.

Material and methods

Study site. The study was conducted at the Parque Estadual de Campos do Jordão, Serra da Mantiqueira, SE Brazil (22° 44' S, 45° 35' W). This montane area is covered mainly by mixed broadleaf and *Araucaria* forest (EITEN 1970). Elevation is about 1500 m s.m.; annual rainfall up to 2000 mm; wet season from October to March; winter temperature may fall below zero from June to August (NIMER 1977, HUECK 1972). *Siphocampylus sulfureus* is found in open, highland marshes and along brooklets at forest borders. Other *Siphocampylus* species found within the study area are *S. cf. betulaefolius* (CHAM.) G. DON and *S. westinianus* (BILLB.) POHL.

Procedure. Field work was done mostly in February and April 1992, and January and March 1993. Phases of anthesis were observed in situ. Pollen viability and receptivity of stigmata were tested using the techniques of germination in 2% sucrose, and H₂O₂ catalase activity, respectively (RADFORD & al. 1974, ZEISLER 1938). Sugar concentration in the nectar was measured with a pocket refractometer and its volume with a microsyringe. Colour names follow KORNERUP & WANSCHER (1963). Vouchers are in the herbarium of the Universidade Estadual de Campinas (UEC 26833, 28016). Our plants fit well the description of *S. sulfureus* var. *glaber* (A. ZAHLB.) E. WIMM. in the sense of WIMMER (1957).

Flowers were initially watched for visitors at different times of the day covering the dawn to dawn period. Later we concentrated our observations from dawn to mid-morning and from mid-afternoon to late night (see "floral biology"). Daytime visitors were watched through binoculars and photographed for analyses of their visiting behaviour (cf. SAZIMA 1977, SAZIMA & al. 1993). Crepuscular and night visitors were observed by skylight or with aid of torches with red filters; photographs were taken to analyse their feeding behaviour (see SAZIMA & al. 1989).

Results

Plant habit and floral biology. *Siphocampylus sulfureus* grows in patches as a herbaceous annual (see GODOY 1992) 2–3 m high, some individuals reaching up to 4 m. Its axillary flowers are relatively short stalked, and arranged in whorls along the stem (Fig. 2 a). The flowers are tubular, gullet-type (cf. FÆGRI & VAN DER PIJL 1980) with cleft lowermost corolla lobe, and well exposed reproductive organs (Fig. 2 b). Flower colours vary from sulfur yellow at the apex to lime green at the base of the corolla. Odour is strong, acrid and musky, reminding that of certain foxes and is more pronounced at dusk and during the night. Plant collectors and local people are well aware of the odour (GODOY 1992, and pers. obs.).

The blooming period of the study population lasted from late December to early April, the flowering peak being January–February, towards the end of rainy season. This timing is characteristic of *S. sulfureus* at other sites as well (TRINTA & SANTOS 1989, GODOY 1992). The flowering period of large individuals lasted about three months. Fruit set under natural conditions was about 100% (Fig. 2 a), which may indicate selfcompatibility.

Flowers open at mid-afternoon (ca. 15:00–16:00 h) in a protandrous condition, with nectar already available. The yellowish white, pulverulent pollen is easily shed at touch. The flowers remain protandrous until the next morning, when the stigma begins to appear. The two large stigmatic lobes open and are receptive by the afternoon, remaining so for about 36 h. In a given whorl there may be flowers in

both male and female conditions (similar events were described for the anthesis of three ornithophilous species of *Siphocampylus* in Argentina, see GALETTO & al. 1993). Nectar is produced from mid-afternoon to mid-morning for three consecutive days. The nectar volume available at a given time per flower varied from 1 to 30 μl (\bar{x} = 14.2, sd = 8.9, n = 22), measured within the period from 16:00 to 22:15 h, and from 1 to 26 μl (\bar{x} = 6.0, sd = 7.4, n = 10) at 07:45 h. After mid-morning until mid-afternoon almost no nectar is available (see FEINSINGER 1978 for variation in nectar secretion in another neotropical lobelioid flower, *Lobelia laxiflora*). Sugar concentration in nectar of *S. sulfureus* varied from 4 to 16% (\bar{x} = 11.5, sd = 3.9, n = 29), with no difference between day and night periods.

Visitors. Three hummingbird species were observed by day on *S. sulfureus* flowers: the White-throated Hummingbird, *Leucochloris albicollis* (VIEILLOT), the Brazilian Ruby, *Clytolaema rubricauda* (BODDAERT), and the Purple-breasted Plovercrest, *Stephanoxis lalandi* (VIEILLOT). *Leucochloris* was the most frequent visitor (> 2 visits/hour), whereas *Stephanoxis* was a sporadic one (< 1 visit/hour). The White-throated Hummingbird was a constant visitor from dawn to mid-morning, and from mid-afternoon to dusk. During its hovering visits the bird touched the flower's reproductive organs with its upper bill and forehead (Fig. 3 a). (In the mid-afternoon the hummingbird probed into the "ripe" buds, which often caused these to open earlier.) The hummingbird probed into each open flower in a whorl consecutively and visited all flowering individuals within a patch of *S. sulfureus*. After these feeding bouts it perched nearby, apparently holding a territory over the patch. The patch-holding bird chased visiting conspecifics, as well as the smaller Purple-breasted Plovercrest, but the larger Brazilian Ruby was unmolested. (Thus, *Leucochloris* played the role of a territorialist, *Stephanoxis* acted as a territory-parasite, and *Clytolaema* seemed a marauder, in the sense of FEINSINGER & COLWELL 1978.)

At dusk and early night the flowers were visited by sphingid moths. One of the most frequent moth visitors was tentatively identified as *Xylophanes xylobates* (BURMEISTER), and another frequent moth was the smaller *X. tersa* (L.). The sphingids probed with their tongue within the open flowers while hovering; during this visit their tongue and head occasionally touched the flower's reproductive organs.

The Geoffroy's Long-nosed Bat, *Anoura caudifer* (E. GEOFFROY), was the only bat visitor recorded on *S. sulfureus* flowers. This bat arrived shortly after the sphingids and circled the flowering plants. During the hovering visit the bat thrust its snout within the corolla, touching the flower's reproductive organs with the top of its head. The cleft, lowermost corolla lobe allowed for the bat's snout reaching deep into the flower (Fig. 3 b). During a feeding bout the bat habitually probed within each open flower in a whorl but not always consecutively, and visited most of the flowering plants within view. The bat also touched with its snout a few larger and presumably "ripe" buds, but we were unable to verify whether these opened later that night.

Two to three individual bats were recognized visiting the observed patches on a given night. Some photographs show one of the bats with its chin covered with orange yellow pollen (quite probably from *Abutilon* aff. *regnellii* K. SCHUM; S. BUZATO, unpubl. results). Intervals between feeding bouts varied greatly even in

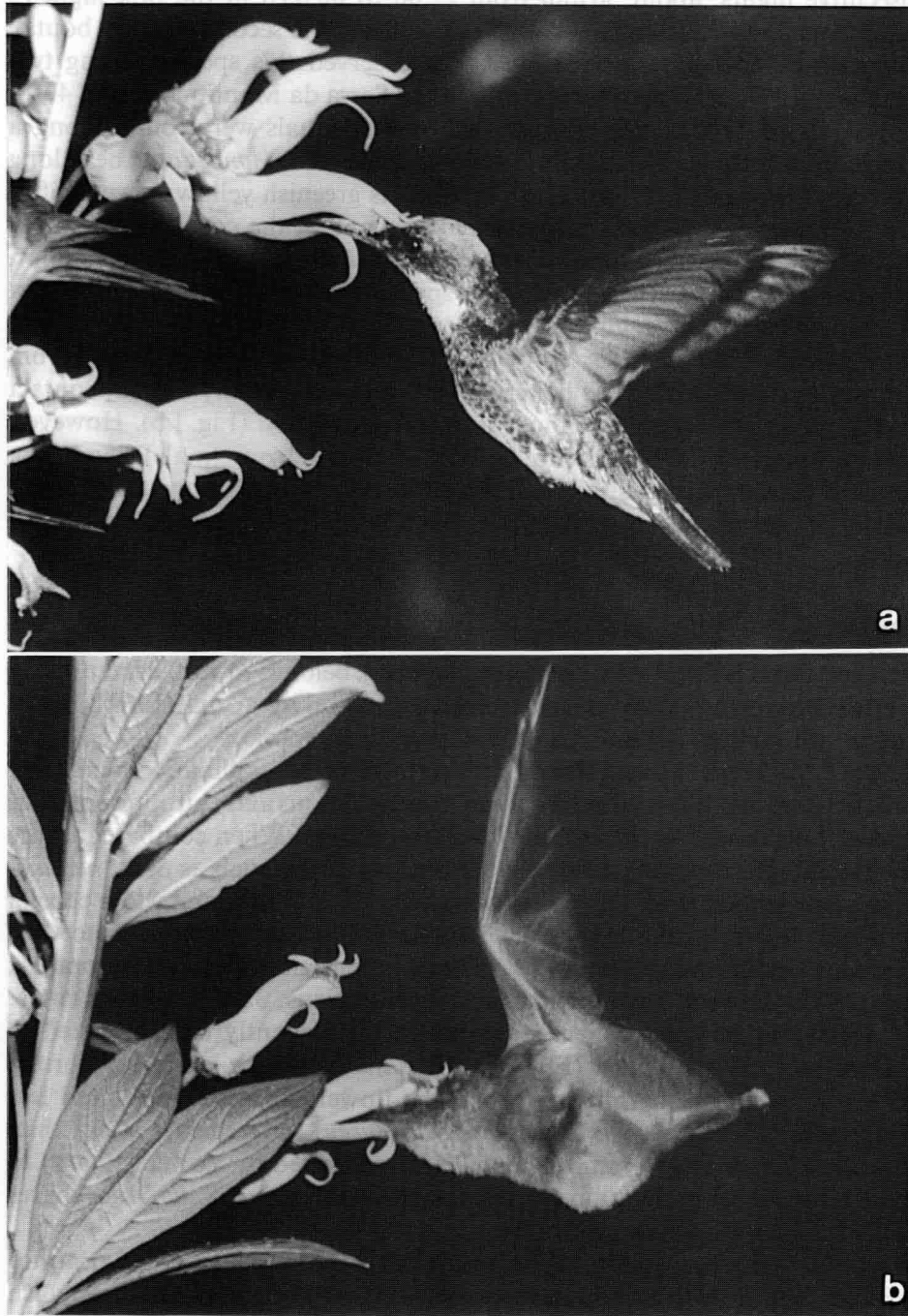


Fig. 3. Day and night pollination of *S. sulfureus*. *a* The White-throated Hummingbird, *Leucochloris albicollis*, at late afternoon (pollen load on bird's crown is from *S. cf. betulaeifolius*, whereas pollen on upper bill and forehead is from *S. sulfureus*). *b* The Geoffroy Long-nosed Bat, *Anoura caudifer*, at early night. Notice cleft lowermost corolla lobe being displaced both by the hummingbird and the bat

two consecutive nights: about 30 min from 22:00 to 00:05 h in the first night (5 bouts), and from 15 to 250 min from 21:05 to 01:30 h in the second night (3 bouts).

Remarks on *Siphocampylus umbellatus*. We observed this species during two days in January 1993, at Camanducaia, also in the Serra da Mantiqueira (22° 46' S, 46° 09' W) at about 1700 m s.m. Two branched individuals were found along a water trickle on a hillside. The terminal inflorescences of *S. umbellatus* bear long stalked flowers (WIMMER 1957, see also Fig. 1 b). Its greenish yellow flowers differ from that of *S. sulfureus* in their larger size, the shape of the corolla apex, more exposed reproductive organs, larger corolla opening (Fig. 2 c), and milder odour. *S. umbellatus* reminded us strongly of some species of *Burmeistera* (see WIMMER 1957), a chiropterophilous genus with Andean distribution (VOGEL 1969 a, b). Flowers of *S. umbellatus* were visited by the White-throated Hummingbird from late afternoon to dusk. During the hovering visits the bird usually did not contact the reproductive organs, especially those in female condition (Fig. 1 b). However, occasional contacts might occur with flowers in protandrous (male) condition. After dusk the flowers were visited by a glossophagine bat (possibly *Anoura*, but no specimen or photo available). After the bat's visits, pollen was found spread on stigmata.

Discussion

Plant habit and floral biology. *Siphocampylus sulfureus* belongs to sect. *Macrosiphon* subsect. *Eusiphocampylus* (WIMMER 1957), which is placed by VOGEL (1969 b, 1980) within the ornithophilous assemblage of *Siphocampylus* species.

However, *S. sulfureus* shows a clear tendency towards bat pollination, and some of its floral features are intermediate between ornithophilous and chiropterophilous syndromes of *Lobelioideae* as presented by VOGEL (1969 a). When compared to the "typical" hummingbird-pollinated species of *Siphocampylus* such as *S. cf. betulae-folius* of the same section (Fig. 1 a), *S. sulfureus* has a shorter tube and wider corolla opening, a cleft lower corolla lobe (Figs. 2 b and 3 a), a yellow colour instead of red, and strong odour and dilute nectar. (Three Argentinian species with orange, or red and yellow flowers, have high sugar concentrations, 32–36%, GALETTO & al. 1993). On the other hand, when compared to the evidently bat-pollinated *S. umbellatus* of sect. *Brachysiphon* (Fig. 1 b), *S. sulfureus* has a narrower corolla opening (Fig. 2), a shorter corolla apex, and the flowers are less sturdy and less oriented upwards. Moreover, the flowers of *S. sulfureus* have shorter stalks than those of *S. umbellatus*. Thus, from the nine features selected by VOGEL (1969 a) to contrast the bird and bat pollination syndromes within the genus, *S. sulfureus* shares about half of them with either syndrome.

Were not for the strong odour *S. sulfureus* might be regarded as an ornithophilous species. The more so as in some cases this plant may be difficult to distinguish from the closely related *S. verticillatus* (CHAM.) G. DON. (Y. HARVEY, pers. comm.), which, however, has not such an odour and its corolla bears no cleft lower lobe (GODOY 1992). The sucrose/hexose ratio of *S. sulfureus* is 1.54 (data calculated from GOTTSBERGER & al. 1984), a ratio regarded as characteristic of hummingbird-pollinated flowers (BAKER & BAKER 1990). Three Argentinian *Siphocampylus* species of sect. *Macrosiphon*, with orange or red and yellow flowers, also present sucrose-dominated nectar, and hummingbird pollination was recorded for one of

them (GALLETO & al. 1993). However, phylogenetic constraints should be regarded as well, since some taxonomic groups may have a tendency to sucrose or hexose richness in their nectar (see PERCIVAL 1961, GOTTSBERGER & al. 1984, BAKER & BAKER 1990). Strangely enough, nectar production in *S. sulfureus* is greater at night and its flowers open at mid-afternoon. Taken all its features together, this yellow-flowered species may be viewed as an intermediate step between the syndromes of bird and bat pollination.

Visitors. Hummingbirds are known to visit several species of chiropterophilous flowers but usually they act as nectar thieves (e.g., SAZIMA & SAZIMA 1975), although in some instances they are occasional or minor pollinators (BAKER & al. 1971, SAZIMA & SAZIMA 1978). However, in *S. sulfureus* we regard hummingbirds as effective or even major pollinators, sharing this role with bats. This is achieved both by the hummingbird visiting constancy and the fitting between the flower and bird morphology.

The clustered distribution of *S. sulfureus* plants concentrates the nectar resource and promotes territorial behaviour of the White-throated Hummingbird, habitually a generalist or a facultative trapliner (in the sense of FEINSINGER & COLWELL 1978). The territoriality keeps most of the pollen carried by this hummingbird within a given patch, thus probably reducing gene flow between patches and lowering variability (STILES 1975, WEBB & BAWA 1983).

We regard sphingid visitors to *S. sulfureus* flowers as minor pollinators in the sense of BAKER & al. (1971). Sphingid moths visiting chiropterophilous flowers act either as nectar thieves or as minor pollinators (e.g., SILBERBAUER-GOTTSBERGER & GOTTSBERGER 1975, SAZIMA & SAZIMA 1978).

Bat visits to *S. sulfureus* flowers follow the pattern recorded for most glossophagines (FLEMING 1982, HEITHAUS 1982, DOBAT & PEIKERT-HOLLE 1985). The visiting behaviour of *Anoura caudifer* on *S. sulfureus* is reminiscent of that described for the bat *Lonchophylla bokermanni* SAZIMA & al. on the inflorescences of the terrestrial bromeliad *Encholirium glaziovii* MEZ (SAZIMA & al. 1989). The *Abutilon* pollen recorded on one *A. caudifer* supports the idea that a given glossophagine individual feeds on several sources throughout its nightly foraging activity (SAZIMA 1976, SAZIMA & al. 1982, LEMKE 1984). The use of diverse food sources throughout the night may partly explain the recorded variability of intervals between *A. caudifer* feeding bouts on *S. sulfureus* flowers.

We recorded *A. caudifer* as the only flower visitor in other montane sites at elevations from 1200 to 1800 m s.m. Although altitudinal distribution of this and other glossophagine bats in SE Brazil remains unstudied, we suspect that *Anoura* stands as the main bat pollinator at elevations above 1000 m. At lower sites, the Pallas Long-tongued Bat, *Glossophaga soricina* (PALLAS), is the most common flower visitor (see comments in SAZIMA & al. 1982, BUZATO & FRANCO 1992).

Hummingbird and bat pollination in *Siphocampylus*. From the about 180 species of *Siphocampylus* sect. *Macrosiphon* most (c. 90%) are coloured red, red and yellow, or orange (data calculated from WIMMER 1957). Hummingbirds were recorded visiting orange, or red and yellow flowers of three species from this section (SNOW & SNOW 1980, SNOW & TEIXEIRA 1982, GALLETO & al. 1993; see also Fig. 1 a). The subsections *Eusiphocampylus* and *Hemisiphocampylus* are regarded as ornithophilous, whereas *Byrsanthes*, the remaining subsection within *Macrosiphon*, is re-

garded as chiropterophilous (see figures in VOGEL 1969 b, 1980). The whole section *Brachysiphon*, here exemplified by *S. umbellatus*, is regarded as bat-pollinated (VOGEL 1969 a, b, 1980).

Among several features regarded as characteristic of the chiropterophilous syndrome, VOGEL (1969 a) pointed out that bat-pollinated species of *Siphocampylus* are taller and sturdier than the ornithophilous ones. Within subsect. *Eusiphocampylus*, *S. sulfureus* fulfills both these requirements notwithstanding the "mixed" nature of its features as a whole. Taken together, the relatively delicate floral morphology, diurnal anthesis, and sucrose-dominated nectar point towards the bird pollination syndrome. On the other hand, the strong odour, night production of dilute nectar, and greenish yellow colour are features related to bat pollination (VOGEL 1969 a, FÆGRI & VAN DER PIJL 1980).

Based on the assumption that chiropterophily is a derived condition within *Siphocampylus* (VOGEL 1969 a, b) we think that *S. sulfureus* may be viewed as a recent derivate from the presumed ornithophilous stock (exemplified by most species of subsect. *Eusiphocampylus*). The opposite view, i.e., that bird pollination is a derived condition within *Siphocampylus* seems less plausible (see figure 7 in VOGEL 1980 for pollination trends within the genera *Burmeistera*, *Centropogon*, and *Siphocampylus*), but trends towards bird or bat pollination may have evolved independently and several times within *Lobeliaceae*. In any case, however, *S. sulfureus* presents both the ornithophilous and chiropterophilous features and thus benefits from the activity of two major pollinators: hummingbirds (diurnal) and bats (nocturnal). Pollinator role sharing by hummingbirds and bats is probably found in some other neotropical plant species as well, but it may have been overlooked because it is disguised by the more prominent features of an ornithophilous or chiropterophilous syndrome.

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References

- BAKER, H. G., BAKER, I., 1990: The predictive value of nectar chemistry to the recognition of pollinator types. — *Israel J. Bot.* **39**: 157–166.
- CRUDEN, R. W., BAKER, I., 1971: Minor parasitism in pollination biology and its community function: the case of *Ceiba acuminata*. — *BioSci.* **21**: 1127–1129.
- BUZATO, S., FRANCO, A. L. M., 1992: *Tetrastylis ovalis*: a second case of bat-pollinated passionflower (*Passifloraceae*). — *Pl. Syst. Evol.* **181**: 261–267.
- DOBAT, K., PEIKERT-HOLLE, T., 1985: Blüten und Fledermäuse (Chiropterophilie). — Frankfurt am Main: Kramer.
- EITEN, G., 1970: A vegetação do estado de São Paulo. — *Bol. Inst. Bot. (São Paulo)* **7**: 1–147.

- FÆGRI, K., VAN DER PIJL, L., 1980: The principles of pollination ecology. 3rd edn. (Reprint with revisions.) – New York: Pergamon Press.
- FEINSINGER, P., 1978: Ecological interactions between plants and hummingbirds in a successional tropical community. – *Ecol. Monogr.* **48**: 269–287.
- COLWELL, R. K., 1978: Community organization among neotropical nectar-feeding birds. – *Amer. Zool.* **18**: 779–795.
- FLEMING, T. H., 1982: Foraging strategies of plant-visiting bats. – In KUNZ, T. H., (Ed.): *Ecology of bats*, pp. 287–325. – New York: Plenum Press.
- GALETTO, L., BERNARDELLO, L. M., JULIANI, H. R., 1993: Estructura del nectario, composición química del nectar y mecanismo de polinización en tres especies de *Siphocampylus* (*Campanulaceae*). – *Kurtziana* **22**: 81–96.
- GODOY, S. A. P., 1992: Flora da Serra do Cipó, Minas Gerais: *Campanulaceae*. – *Bolm. Botânica, Univ. São Paulo* **13**: 241–257.
- GOTTSBERGER, G., SCHRAUWEN, J., LINSKENS, H. F., 1984: Amino acids and sugar in nectar, and their putative evolutionary significance. – *Pl. Syst. Evol.* **145**: 55–77.
- HEITHAUS, E. R., 1982: Coevolution between bats and plants. – In KUNZ, T. H., (Ed.): *Ecology of bats*, pp. 287–325. – New York: Plenum Press.
- HUECK, K., 1972: As florestas da América do Sul. – São Paulo: Editora Polígono.
- KORNERUP, A., WANSCHER, J. H., 1963: Taschenlexikon der Farben. – Zürich, Göttingen: Musterschmidt.
- LEMKE, T. O., 1984: Foraging ecology of the long nosed bat, *Glossophaga soricina*, with respect to resource availability. – *Ecology* **65**: 538–548.
- NIMER, E., 1977: Climatologia da região sudeste do Brasil. – *Rev. Brasil. Geogr.* **34**: 3–48.
- PERCIVAL, M. S., 1961: Types of nectar in angiosperms. – *New Phytol.* **60**: 235–281.
- RADFORD, A. E., DICKSON, W. C., MASSEY, J. R., BELL, C. R., 1974: Vascular plant systematics. – New York: Harper & Row.
- SAZIMA, I., 1976: Observations on the feeding habits of phyllostomatid bats (*Carollia*, *Anoura*, and *Vampyrus*) in SE Brazil. – *J. Mammal.* **57**: 381–382.
- BUZATO, S., SAZIMA, M., 1993: The bizarre inflorescence of *Norantea brasiliensis* (*Marcgraviaceae*): visits of hovering and perching birds. – *Bot. Acta* **106**: 507–513.
- VOGEL, S., SAZIMA, M., 1989: Bat pollination of *Encholirium glaziovii*, a terrestrial bromeliad. – *Pl. Syst. Evol.* **168**: 167–179.
- SAZIMA, M., 1977: Hummingbird pollination of *Barbacenia flava* (*Velloziaceae*) in the Serra do Cipó, Minas Gerais, Brazil. – *Flora* **166**: 239–247.
- SAZIMA, I., 1975: Quiropterofilia em *Lafoensia pacari* ST. HIL. (*Lythraceae*), na Serra do Cipó, Minas Gerais. – *Ciênc. Cult.* **27**: 405–416.
- – 1978: Bat pollination of the passion flower, *Passiflora mucronata*, in SE Brazil. – *Biotropica* **10**: 100–109.
- FABIAN, M. E., SAZIMA, I., 1982: Polinização de *Luehea speciosa* (*Tiliaceae*) por *Glossophaga soricina* (*Chiroptera, Phyllostomidae*). – *Rev. Brasil. Biol.* **42**: 505–513.
- SILBERBAUER-GOTTSBERGER, I., GOTTSBERGER, G., 1975: Über sphingophile Angiospermen Brasiliens. – *Pl. Syst. Evol.* **123**: 157–184.
- SNOW, D. W., SNOW, B. K., 1980: Relationships between hummingbirds and flowers in the Andes of Colombia. – *Bull. Brit. Mus. Nat. Hist. (Zool.)* **38**: 105–139.
- TEIXEIRA, D., 1982: Hummingbirds and their flowers in the coastal mountains of SE Brazil. – *J. Ornith.* **123**: 446–450.
- STILES, F. G., 1975: Ecology flowering phenology and hummingbird pollination of some Costa Rican *Heliconia* species. – *Ecology* **56**: 285–301.
- TRINTA, E. F., SANTOS, E., 1989: Campanuláceas. Flora ilustrada catarinense, Parte I. 75p. – Itajaí, Santa Catarina: Edit. Herb. “Barbosa Rodrigues”.

- VOGEL, S., 1969 a: Chiropterophilie in der neotropischen Flora (Neue Mitteilungen II). – Flora **158**: 185–222.
- 1969 b: Chiropterophilie in der neotropischen Flora (Neue Mitteilungen III). – Flora **158**: 289–323.
- 1980: Florengeschichte im Spiegel blütenökologischer Erkenntnisse. – Rheinisch-Westfälische Akad. Wiss. **291**. – Opladen: Weltdeutscher Verlag.
- WEBB, C. J., BAWA, K. S., 1983: Pollen dispersal by hummingbirds and butterflies: a comparative study of two lowland tropical plants. – Evolution **37**: 1258–1270.
- WIMMER, F. E., 1957: *Campanulaceae-Lobelioideae*, H. 107. – In ENGLER, A., DIELS, L., (Eds): Das Pflanzenreich, pp. 261–813. – Berlin: Akademie.
- ZEISLER, M., 1938: Über die Abgrenzung der eigentlichen Narbenfläche mit Hilfe von Reaktionen. – Beih. Bot. Zentralbl. **58**: 308–318.

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