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Dyssochroma viridiflorum (Solanaceae): a Reproductively Bat-dependent Epiphyte from the Atlantic Rainforest in Brazil

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Few Neotropical plant species seem to depend on the same animal type both for pollination and seed dispersal, and the known instances refer mostly to birds as the agents in these two phases of a plant reproductive cycle. *Dyssochroma viridiflorum* (Solanaceae), an epiphyte endemic to the Atlantic rainforest in south-eastern Brazil, was found to be visited by phyllostomid bats for nectar as well as for fruits, with the pollination and seed dispersal of the plant ensured by these flying mammals. The greenish flowers open at night and are visited by the nectar-feeding bat *Glossophaga soricina*, whereas the yellowish-white fruits are consumed by two species of fruit-eating bats, *Carollia perspicillata* and *Sturnira lilium*. Only clinging visits, an uncommon behavioural pattern for glossophagine bats while feeding on flowers, were recorded. The small seeds of *D. viridiflorum* are swallowed along with the fruit pulp and later defecated on the bats' flying pathways. It is suggested that species of *Dyssochroma* and two other solanaceous bat-pollinated genera, *Merinthopodium* and *Trianaea*, form a derived and bat-dependent clade within the Juanulloeae.

Key words: *Dyssochroma*, Solanaceae, reproduction, bat-pollination, *Glossophaga,* bat-dispersal, *Carollia*, *Sturnira*, Phyllostomidae, rainforest, south-eastern Brazil.

INTRODUCTION

Few Neotropical plant species seem to depend on the same animal type both for pollination and seed dispersal, and the known cases refer mostly to birds as the agents in these two phases of a plant reproductive cycle. For instance, species of Bromeliaceae and Costaceae are pollinated mainly by hummingbirds, and dispersed by passerine birds and small mammals in south-eastern Brazil (Fischer and Araujo, 1995; Buzato *et al.*, 2000; I. Sazima, pers. obs.). As the distribution of bat flowers and fruits among orders of angiosperms is remarkably concordant (Fleming, 1988) it would be expected that these would be found within the same orders, families, and in certain cases, even genera. Indeed, some species of Cactaceae in Central and northern South America are pollinated and, to some extent, dispersed by phyllostomid bats (e.g. Petit, 1997; Martino *et al.*, 2002). It was observed that *Dyssochroma viridiflorum* (Sims) Miers, an epiphytic solanaceous plant endemic to the Atlantic rainforest in south-eastern Brazil, southern South America (Hunziker, 1979; Knapp *et al.*, 1997), also has its flowers pollinated and its seeds dispersed by phyllostomid bats. *Dyssochroma* belongs in the tribe Juanulloeae, a group composed of six genera of poorly known, rarely collected epiphytic shrubs and small trees distributed over the Neotropics (Knapp *et al.*, 1997). However, Olmstead *et al.* (1999) and Hunziker (2001) recognize nine genera in this group. Within Juanulloeae (Juanulloinae of Olmstead *et al.*, 1999), species of *Dyssochroma*, *Merinthopodium* and *Trianaea* are recorded as, or supposed to be, pollinated by bats (Vogel, 1958; Baker, 1973; Voss *et al.*, 1980; Dobat and Peikert-Holle, 1985; Knapp *et al.*, 1997). For present taxonomic allocation of several genera and species presented in earlier papers and referred to herein, see Olmstead *et al.* (1999) and Hunziker (2001).

Here the floral biology and bat-pollination, as well as bat-frugivory and seed dispersal of *Dyssochroma viridiflorum* is described, and it is predicted that species in the other two bat-pollinated genera of Juanulloeae, *Merinthopodium* and *Trianaea*, may prove to be bat-dispersed as well.

MATERIALS AND METHODS

The study sites are in the coastal lowlands covered by sub-humid evergreen broadleaf forest (Eiten, 1970; Sazima *et al.*, 1999) at Picinguaba (about 23°20′S, 44°52′W, 0–10 m a.s.l.) and Praia Dura (about 23°30′S, 45°07′W, at sea level) in Ubatuba, São Paulo, south-east Brazil. Average annual rainfall at the study sites is 2526 mm, and average annual temperature is 22·7 °C (Sazima *et al.*, 1999; Buzato *et al.*, 2000). The bulk of data on plants and bats was obtained during two nights in March and two nights in April 1998, with supplementary data on flowers and fruits recorded from March 2001 to December 2002. The growth habit, flowering phenology and flower features such as morphology, phases of anthesis, colour, odour, volume and concentration of

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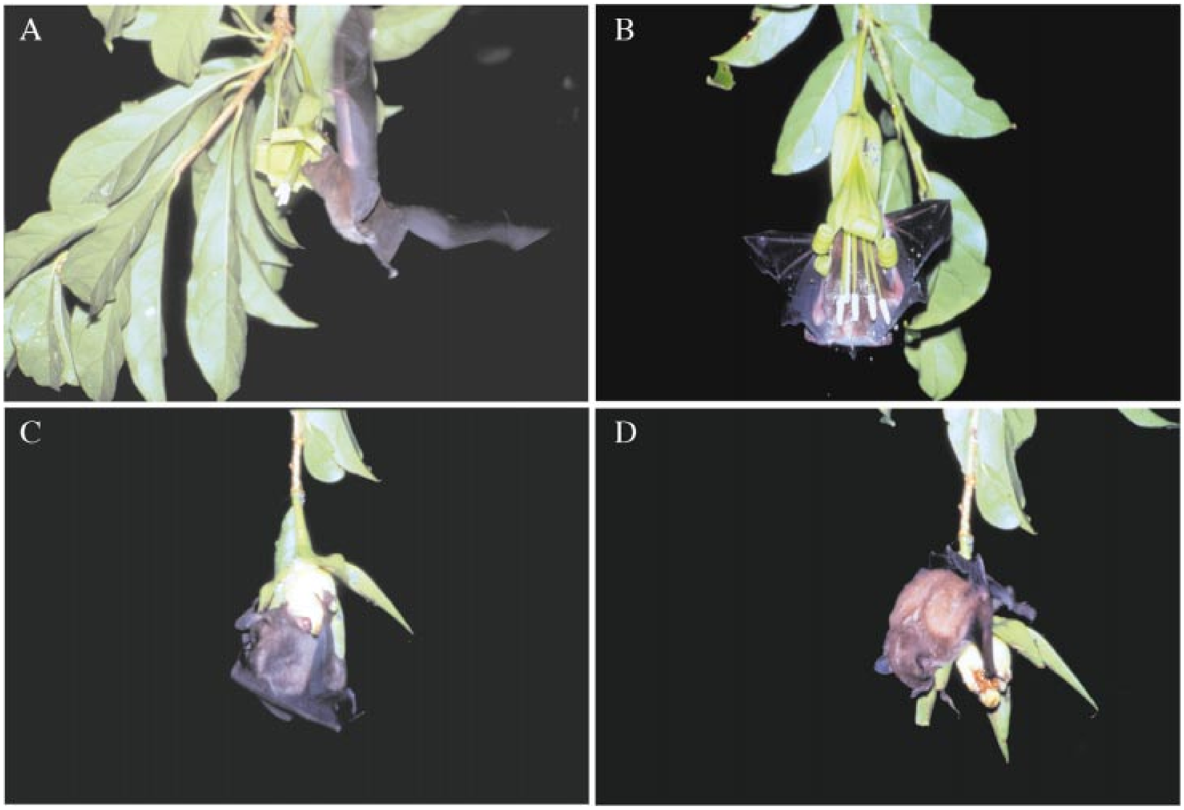

FIG. 1. A, *Glossophaga soricina* about to visit a newly opened flower. Note the downward orientation of *Dyssochroma viridiflorum* flowers with both stamens and style exerted beyond the corolla opening, and whitish pollen from previous visits on the bat belly. B, The same bat species clinging to an already visited first-day flower. Note the bat left wing claw grasping the flower, the claw marks on the corolla, and the anthers touching the bat hind-body. C, *Carollia perspicillata* biting off a piece of a ripe fruit. Note the bat feet grasping the fruit. D, *Sturnira lilium* about to bite off a piece of an already chewed fruit. Note yellowish white pulp and brownish, small seeds.

nectar were recorded (cf. Faegri and Pijl, 1980; Sazima *et al*., 1999). The phenology was recorded monthly on a pool of 17 individuals to characterize the flowering of the studied population (cf. Newstrom *et al*., 1994). The internal length of the flower corolla was measured from base to opening (effective length; cf. Wolf *et al*., 1976). Nectar concentration and volume were measured 2 h after flower opening (visitors excluded from measured flowers), with a pocket refractometer and microlitre syringes, respectively (cf. Kearns and Inouye, 1993). Nectar scent was assessed *in situ* and out of the flower (flowers with no nectar are odourless). Flower shape nomenclature follows Faegri and Pijl (1980). Fruit and seed features such as morphology, colour, shape, and size were also recorded. Colour names of flowers, fruits and seeds follow Kornerup and Wanscher (1963). Stigma receptivity was tested by the H_2O_2-catalase activity method (Zeisler, 1938) and pollen viability was estimated by cytoplasmic staining, using the aceto-carmine technique (Radford *et al*., 1974). Controlled pollinations were performed on eight individual plants in order to establish the breeding system following methods outlined in Radford *et al*. (1974). Fruit set was recorded on maturing fruits. For pollen tube growth, fixed hand-pollinated pistils were analysed under fluorescence microscopy (Martin, 1959). Plant vouchers are deposited in the herbarium of the Universidade Estadual de Campinas (UEC 119286, 119287). Bats were photographed on flowers and fruits during visits and species identification was based on photographs. Species recognition at a well-studied site may be very reliable even at species level (see Sazima and Sazima, 1977; Sahley, 1995; Sazima *et al*., 1999), and depends on a good knowledge of species occurring in the area. Photographs of bat visits on flowers were used to assess pollen placement on the body parts of bats, and mist-netted individuals were examined for seed loads in their faeces.

RESULTS AND DISCUSSION

Plant habit, phenology, flower features and floral biology

At the study sites *Dyssochroma viridiflorum* occurs mainly as a saxicolous (rock-dwelling) shrub near the seashore or as an epiphyte on various tree species. Saxicolous habit is not mentioned by Knapp *et al*. (1997), but seems to be a common feature for this species in the lowland rainforest (Hunziker, 1979, 2001). It was found that, at the study sites, *D. viridiflorum* blooms year-round, a phenological pattern defined as continual by Newstrom *et al*. (1994). Such a phenological pattern is unusual in Neotropical bat-pollinated species and until now it has been recorded for

Marcgravia serrae (Marcgraviaceae) in Costa Rica (Tschapka and Helversen, 1999), and for *Marcgravia polyantha*, *Abutilon* aff. *regnellii* (Malvaceae) and *Irlbachia alata* (Gentianaceae) in Brazil (Machado *et al.*, 1998; Sazima *et al.*, 1999). A given *D. viridiflorum* individual may bear buds, open flowers, developing fruits and ripe fruits at the same time, thus providing night meals for both nectarivorous and frugivorous bats (see below). One individual may produce one to ten flowers per night, a trait which promotes the trapline mode of foraging and seems widespread amongst bat-pollinated species (Heithaus *et al.*, 1975; Sazima *et al.*, 1999). Inflorescences are terminal, which agrees with the records of Knapp *et al.* (1997), and bear one to four flowers at a time. Mostly one and, occasionally, two open flowers per inflorescence per night were found, a common trait in the bat-pollinated species of *Merinthopodium* and *Trianaea* (Solanaceae) (Vogel, 1958, 1969; Voss *et al.*, 1980), as well as in several other bat-pollinated species (e.g. *Irlbachia alata*, Machado *et al.*, 1998; *Vriesea* spp., Bromeliaceae, Sazima *et al.*, 1999). Peduncles of *D. viridiflorum* are short (30–40 mm), and the flowers point downwards (Fig. 1A and B). Such an orientation in Neotropical bat-pollinated flowers is uncommon, but it is known also to occur in species of the two other solanaceous genera, *Merinthopodium* and *Trianaea* (Voss *et al.*, 1980; Knapp *et al.*, 1997).

The broadly flaring to campanulate corolla of *D. viridiflorum* (Fig. 1A and B) has an average effective length of 63·7 mm (s.d. = 5·7, *n* = 10), and the average largest diameter of the corolla opening is 30 mm (s.d. = 3·5, *n* = 10). The corolla is greenish externally and yellowish-green internally, both stamens and style being green and exerted to about the same level, well beyond the corolla opening (Fig. 1A and B) even in flowers in post-flowering stage. There are no modifications in the position of the sexual organs during flowering. Filaments are hairy at the lower quarter of its length, a device which may prevent the nectar from dropping by holding it through capillary forces, as recorded in other pendulous bat-flowers (e.g. *Merinthopodium*; see Helversen, 1993). Anthers are large (10–18 mm), and dehisce longitudinally to expose copious, whitish, and somewhat sticky pollen. The style is glabrous, and the green, clavate stigma is placed in the middle of the anthers (Fig. 1B). Morphological features of the flowers fit well into the description of Hunziker (2001) and Knapp *et al.* (1997), although the latter authors note that filaments are glabrous along their whole length.

Young buds of *D. viridiflorum* are protected by the calyx and immersed in watery fluid, the so-called water calyces which occur in some Solanaceae and related families (Endress, 1994). Buds in pre-anthesis are swollen and open in a popping-like way, the corolla lobes moving very quickly, becoming strongly flexed in about 2 min (Fig. 1A and B). The flowers open nearly synchronously around nightfall (1830 h), but sometimes flower opening was delayed until early night, at 2000 h, mostly on cold nights. Flowers last two nights, a feature recorded for a number of other glossophagine-pollinated species (Helversen, 1993; Machado *et al.*, 1998; Sazima *et al.*, 1999). Nectar is available in the flower upon opening and has a mushroom-like scent [Hunziker (2001) notes that flowers are 'perfumed'], scented nectar being recorded for several chiropterophilous plant species (Sazima *et al.*, 1999).

TABLE 1. *Fruit set from autonomous, manual self-pollinated and open-pollinated* Dyssochroma viridiflorum *flowers*

Treatments	Fruit set (%)
Autonomous self-pollination	0 (0/17)
Manual self-pollination	0 (0/12)
Open pollination	72 (18/25)

Figures in parenthesis are number of fruits/number of flowers.

Mean nectar production and concentration of *D. viridiflorum* is about the same on the first and the second nights, respectively: volume 189·8 ± 117·5 µL (*n* = 10) and 189·0 ± 128·7 µL (*n* = 5), concentration 21·7 ± 2·7 % (*n* = 10) and 18·2 ± 2·01% (*n* = 5). The nectar concentration range is slightly above the average of the frequency distribution presented by Helversen (1993) for 33 neotropical bat-pollinated species. During daytime, the available nectar is taken by the hummingbird *Eupetomena macroura*, which pierces the corolla base. The long corolla of *D. viridiflorum* prevents this hummingbird from legitimately visiting the flowers, and thus it does not act as a pollinator as recorded for other non-ephemeral chiropterophilous flowers (Buzato *et al.*, 1994; Sazima *et al.*, 1994).

The stigmatic surface is receptive on flower opening and remains so throughout the second night. Pollen is available on flower opening, easily shed at touch, and most of it is depleted during the first night. Pollen viability is about 93 % throughout the two nights of anthesis. Fruit set from open pollinations (natural conditions) is high, about 70 %, which indicates that bats are able pollen vectors since *D. viridiflorum* is self-incompatible, a trait confirmed by hand-pollination treatments (Table 1). In spite of the pollen tubes' development along the style (Fig. 2A), rejection of self-pollen may occur very late within the ovules in some species of Solanaceae (Aguilar and Bernardello, 2001), and this may indeed be the case in *D. viridiflorum*. Further studies may indicate the presence of an ovarian self-incompatibility system in this species.

Fruits ripen in 30–35 d, during which period they are fully covered by the calyx lobes. Ripe fruits are conical, yellowish-white berries, and completely exposed by the very fleshy flexed calyx lobes (Fig. 2B). Thus, the exposed fruits may be detected by the two bat species by both olfaction (long-distance) and echo-location (short-distance) (see Thies *et al.*, 1998). Fruits are 25–30 mm long, 20–25 mm at greatest diameter, and have a sweet, tomato-like scent. Each berry produces many brown reniform seeds which are 2 × 4 mm. Morphological features of the fruit and seeds studied are essentially the same as those described by Hunziker (2001), and do not differ substantially from those of the other, probably bat-dispersed species of *Trianaea* and *Merinthopodium* (Knapp, 1997).

Bat visits to flowers and fruits

Three phyllostomid bat species were recorded visiting *Dyssochroma viridiflorum*, one species visiting the flowers, and two species feeding on the ripe fruits. The flower-visitor was the ubiquitous long-tongued bat *Glossophaga soricina* (Glossophaginae) (Fig. 1A and B), and the fruit-eaters were the short-tailed bat *Carollia perspicillata* (Carolliinae) (Fig. 1C), and the yellow-shouldered bat *Sturnira lilium* (Stenodermatinae) (Fig. 1D). Glossophagines are small bats with a manoeuvrable flight well suited to taking nectar from flowers, whereas carolliines and stenodermatines are slightly larger and heavier, but nevertheless still suited to taking fruits from delicate branches or visit flowers for nectar (Sazima 1976; Sazima and Sazima, 1978; Heithaus, 1982; Sazima *et al*., 1999).

The first bats arrive at the flowering and fruiting plants at nightfall (1820–1830 h). After complete flower opening (1830–2000 h), long-tongued bats start visiting the flowers. On the first visit, the bat makes a flight pass close to the flower, these passes being repeated over the night and interspersed with visits to the sampled flower (for scented nectar as a clue for bats, see Sazima *et al*., 1999). This reconnaissance may indicate that the bats are continually assessing the state of a given flower. Alternatively, the bats may be assessing conspecific odour signals, which would indicate that a given flower was recently visited by another bat. Both behaviours would minimise overlap in the use of the same flower's resource (Lemke, 1984; Buzato *et al*., 1994).

During the actual visit, the long-tongued bat approaches the flower from below and clings on to it, while tucking its snout into the corolla (Fig. 1A and B). During the clinging visit the bat's wing claws grasp the flower and pierce the corolla walls, leaving clearly visible marks ('Krallenspuren' of Vogel, 1958, 1969). The claw marks are useful in assessing the number of visits to a given flower (as the bat does not change position while on the flower) and are still used as indirect evidence of bat visits to a given flower species (e.g. Helversen, 1993; for similar marks left by hummingbirds, see Buzato *et al*., 1994). The clinging visit is brief (about 500 ms), during which time the bat hangs on the flower, its feet bent and the interfemural membrane folded backwards, probably so as not to be spoiled further with pollen (Fig. 1B). The bat leaves the flower by releasing its grasp on the corolla and letting itself drop a little (most likely in order to gain free space) before resuming flight.

The bats' clinging visits to *D. viridiflorum* are probably because of the combination of a long corolla and a pendulous, vertical position making it difficult to take nectar while hovering below the flower. At flowers with an even longer corolla, such as those of *Hillia illustris* (about 62 mm), the long-tongued bats are able to take nectar while hovering (Sazima *et al*., 1999). Thus, pictures of bats hovering below flowers of *Trianaea* spp. (Baker, 1973; Helversen 1993; Walker, 2001, the two latter as *Markea*) show the approach phase either of a clinging or a hovering visit. It is predicted that other pendulous and long-flowered, bat-pollinated species in Juanulloeae are visited in a way similar to that described here for *Dyssochroma*.

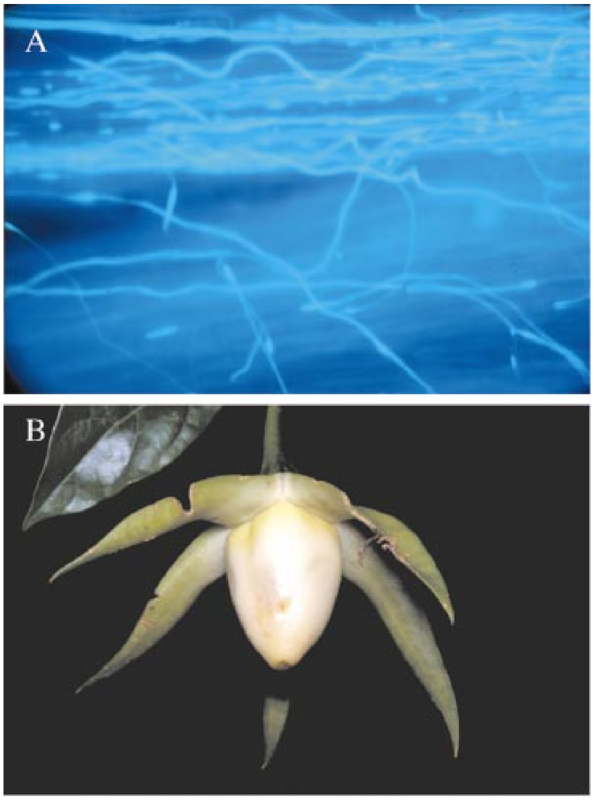

FIG. 2. A, Self-pollen tubes growing along the style. B, A ripe fruit of *D. viridiflorum* exposed by the very fleshy, flexed calyx lobes which totally hide the berry until it is ripe.

The first visit to a *D. viridiflorum* fruit is similar to that on a flower, as the bat makes a close flight pass before the first actual contact (for similar findings, see Kalko and Condon, 1998; Thies *et al*., 1998). As the fruit is scented, it is quite probable that during the pass the bat evaluates the state of a given fruit, including its ripeness and accessibility on the branch (Fleming *et al*., 1977; Thies *et al*., 1998). Additionally, the flexed calyx exposes the fruit making it accessible to echo-location reconnaissance (Kalko and Condon, 1998).

The actual visits differ between the two bat species, as *Carollia perspicillata* habitually approaches the fruit from below and lands on it directly, clinging to the fruit head-up with use of its wing and feet claws (Fig. 1C), whereas *Sturnira lilium* approaches the fruiting branch from above, lands on it and clings on to both the branch and the fruit head-down (Fig. 1D). These two approaches may reflect the flying ability of the two bats, as *Carollia* has a manoeuvrable flight comparable to that of *Glossophaga* (Sazima, 1976; Sazima and Sazima, 1978), whereas *Sturnira* displays a less manoeuvrable flight, similar to that of other small to medium-sized fruit-eating stenodermatines (Heithaus *et al*., 1975; Sazima and Sazima, 1975).

From these different postures, both bat species habitually chew off a piece of the fruit within a very short visit (1–2 s) and leave the fruit in a way similar to the flower visit described for the long-tongued bat. Faeces of bats caught with mist nets, as well as faeces sprayed over the vegetation and boulders contained up to 11 seeds from *D. viridiflorum* per sample, along with seeds from *Piper* spp. (Piperaceae) and *Solanum* spp. (Solanaceae).

A given flower on a *D. viridiflorum* plant was visited at 20–60-min intervals by one or two individual bats, in about four to six visits over a 4-h period. On the other hand, a given fruit was visited in pulses composed of a series of repeated landings by one to four individual bats flying around the plant and succeeding each other, interspersed by 5–15-min intervals, in about 30–40 visits until completely eaten away in about 1 h. *Dyssochroma viridiflorum* offers few flowers and/or fruits per night and is attended by two bat groups with different foraging strategies. Glossophagine bats are regarded as foraging along a trapline route (Baker, 1973; Fleming, 1982; Lemke, 1984), a pattern well suited for most bat-pollinated species in the Atlantic rainforest (Sazima *et al*., 1999). On the other hand, stenodermatine and carolliine bats usually forage by commuting from one food source to another, and may feed in groups (Heithaus *et al*., 1975; Fleming *et al*., 1977; Fleming, 1982). As one fruit of *D. viridiflorum* may be consumed in about 1 h, and as there are no more than two fruits per plant, this plant offers a very limited food supply to fruit-eating bats. The small seeds of *Dyssochroma* are easily swallowed along with the pulp by small fruit-bats such as *Carollia* and *Sturnira* and dispersed along their flying paths, in a fate similar to other small-seeded plants such as *Cecropia* (Cecropiacae) and *Piper* (Heithaus *et al*., 1975; Heithaus, 1982; Fleming, 1982).

Concluding remarks

Most, if not all, species of *Markea* recorded as bat-pollinated (Vogel, 1958; Voss *et al*., 1980; Dobat and Peikert-Holle, 1985; Walker, 2001) are presently merged within either the genera *Merinthopodium* or *Trianaea* (Knapp *et al*., 1997). Most probably there is not a bat-pollinated *Markea*, the species of this genus being pollinated by hummingbirds or insects (Vogel, 1969; Cocucci, 1999). The clade containing *Dyssochroma*, *Merinthopodium* and *Trianaea* (all three genera with bat-pollinated species), is regarded as one of the most derived within Juanulloeae (Knapp *et al*., 1997). The sister-group *Juanulloa parviflora* and the next clade, composed of *J. speciosa* and *J. ochracea*, conform to the hummingbird-pollination habit (Knapp *et al*., 1997). This situation seems to strengthen the hypothesis that several Neotropical bat-pollinated plant groups evolved from bird-pollinated ancestors, an idea supported by studies by several authors (e.g. Vogel, 1969, 1980; Gottsberger, 1972, 1986; Sazima and Sazima, 1988; Buzato *et al*., 1994; Sazima *et al*., 1994).

Judging from literature accounts of bat visits to flowers of *Trianaea* and *Merinthopodium* (Vogel, 1958; Baker, 1973; Voss *et al*., 1980; Walker, 2001) and description of their fruits (Knapp *et al*., 1997), species in these two genera share phyllostomid bats with *Dyssochroma* for pollination and seed dispersal (e.g. Dinerstein, 1986). Thus, it is suggested that these three genera probably form a derived, bat-dependent clade within the Juanulloeae (Knapp *et al*., 1997). Molecular studies may strengthen or weaken this hypothesis.

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