

Observations on the Pollination of *Passiflora penduliflora*¹

Key words: bat; Caribbean; Jamaica; Monophyllus; Passiflora; pollination; savanna; Trochilus.

MEMBERS OF THE GENUS *PASSIFLORA* (PASSIFLORACEAE) are usually pollinated by insects, especially large bees and wasps. Hummingbird pollination is the second most prevalent syndrome in the genus (Janzen 1968, MacDougal 1994). In 1978, bat pollination was reported for the first time in *Passiflora mucronata*. This Brazilian species is pollinated by the phyllostomid *Glossophaga soricina* (Sazima & Sazima 1978). Only one other genus in the family Passifloraceae has been reported as bat-pollinated, with *G. soricina* the major pollen vector of *Tetrastylis ovalis* (also from Brazil; Buzato & Franco 1992).

Both *P. mucronata* and *T. ovalis* exhibit most of the characters associated with a bat-pollination syndrome, including the lack of bright floral pigmentation patterns, the release of an unpleasant odor, and nocturnal anthesis (Faegri & Van Der Pijl 1976, Sazima & Sazima 1978, Buzato & Franco 1992). More recently, *Passiflora penduliflora*, found only in Cuba and Jamaica (Killip 1938, Liogier 1953, Adams 1972), was identified as another likely candidate for bat pollination. *Passiflora penduliflora* is 1 of 11 closely related Greater Antillean endemic species, which are primarily hummingbird-pollinated (Killip 1938, MacDougal 1994); however, unlike the red, unscented tubular flowers of the hummingbird-pollinated species, *P. penduliflora* has lime green, campanulate to slightly tubular flowers that hang upside down from unusually long peduncles. These flowers open up in the early evening and close by early morning. They release copious pollen and have a musty odor (Kay 1999). To interpret the pollination system of *P. penduliflora*, recent observations are presented here on its floral biology in relation to the behavior of its floral visitors and their capacity to carry pollen of the host flower.

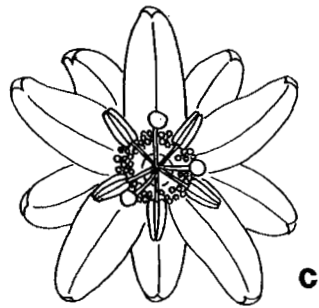
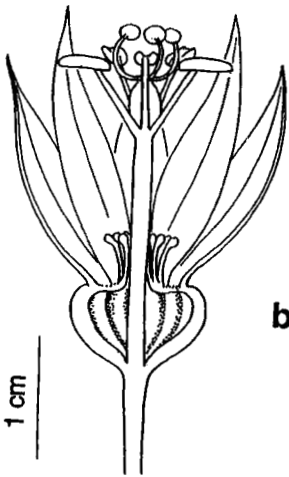
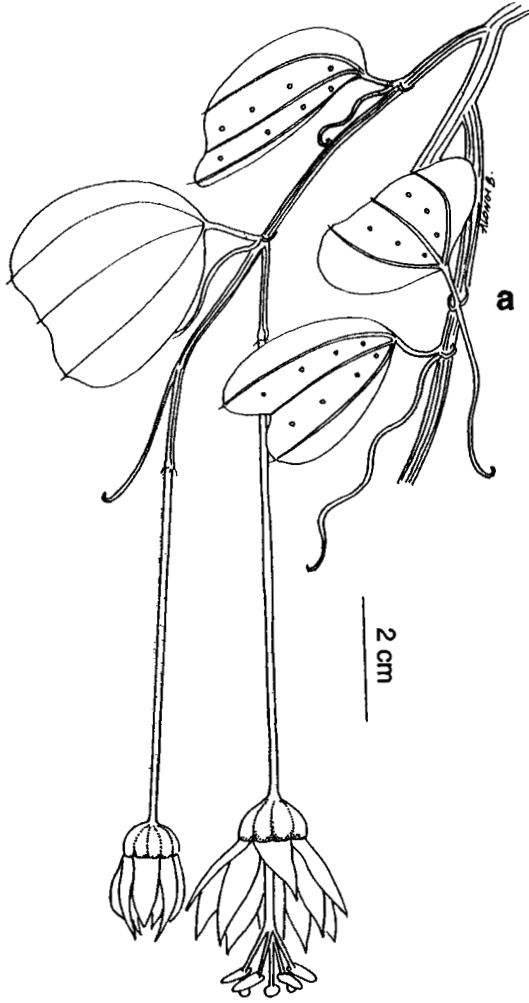
Observations on *P. penduliflora* were conducted at the Mason River Reserve, a wet savanna in Clarendon, Jamaica (Proctor 1970), for 23.5 hours over two days in August 1998 and six days in June/July 1999. A flashlight covered with red cellophane and moonlight provided the only illumination for the early evening and night observations. Mode and frequency of visitation by potential pollinators, as well as changes in the position of different floral organs over the life span of individual labeled flowers were recorded (Buzato & Franco 1992). The concentration of dissolved solutes in nectar was measured in the early evening and early morning using a 0 to 50 percent Bellingham and Standley refractometer (Knox *et al.* 1985). Flowers were smelled *in situ* and by placing four open flowers in a clean, sealed glass jar for a few minutes (Kearns & Inouye 1993).

Bats were caught using 36 mm mist nets and dabbed for pollen using double-sided sticky tape before releasing the animals unharmed (Knox *et al.* 1985). Mist-netting time totaled 24 hours over seven days in June/July 1999 at the Mason River Reserve and surrounding areas; however, bats were caught on two nights only. The sticky tape used to remove pollen from the bats was stained with Calberla's fluid (Ogden *et al.* 1974) for pollen identification under light microscopy. A honeybee, *Apis mellifera*, was netted during daylight hours and sacrificed. Pollen carried by the bee was removed with an ethanol wash and stained with Calberla's fluid for identification (Goldblatt *et al.* 1998).

The inverted buds of *P. penduliflora* opened up in the early evening, exposing a reduced, green corona with orange-tipped filaments that clasped the androgynophore tightly. This ensured that the nectar remained in the flower receptacle, even though the flowers hung upside down (Fig. 1a). Flowers opened once and had a life span of less than 24 hours since petals opened as early as 1600 h, and all floral organs collapsed by early morning between 0600 and 0700 h. The flowers hung clear of the foliage on very long peduncles, which can be 2–4 cm long at anthesis and 6–10 cm long and pendulous in fruit (Killip 1938).

Both anther dehiscence and nectar secretion started between 1630 and 1800 h. The nectar data show that individual flowers contained nectar with a higher concentration of dissolved solutes in the early evening than in the early morning. In the early evening, flowers secreted nectar with a mean of 17.3 percent dissolved solutes (min = 12%, max = 22%, $N = 7$, $SD = 3.2$) but by early morning, flowers

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secreted nectar with a mean of 12 percent dissolved solutes (min = 9%, max = 16%, $N = 17$, $SD = 1.8$).

When the petals had just opened up, the stigmas and styles were close to each other and pointed downward, away from the perianth. The anthers dehisced and were the first sex organs to move toward the perianth (male phase; Fig. 1b). The stigmas did not begin to spread outward until at least an hour later, between 1730 and 1900 h usually, suggesting protandry. At the female phase, anthers and stigmas fully extended outward and pointed down toward the ground (Fig. 1c). Due to the inverted nature of the flowers, this position is probably the most efficient for pollen removal from the anthers and deposition onto the stigmas by pollinators. Open flowers collected in a glass jar at 1900 h emitted a very faint musty odor after 15 minutes. Flowers started closing after 2400 h and were usually fully closed between 0600 and 0700 h, with the stigmas once more clasped together and the anthers fully collapsed.

Two insects were observed visiting *P. penduliflora* flowers. The first was a honeybee (*A. mellifera*) at 1820 h, which actively collected pollen from the dehiscent anthers of the flowers but never touched the stigmas. The corbicular loads removed from the collected bee consisted solely of *P. penduliflora* pollen. These observations suggest that *A. mellifera* is a pollen robber. The second insect observed visiting the flowers ca 1920 h was an uncollected sphingid moth. This single moth visited several open flowers on one plant, drinking nectar for three to five seconds from each flower. It was impossible to see if the moth contacted stigmas and anthers on open flowers given the lighting and distance from the observation point. Therefore, it is possible that moths are infrequent pollinators of *P. penduliflora*.

The two most frequently recorded visitors to *P. penduliflora* flowers were hummingbirds and bats. Both male and female Red-billed Streamertail Hummingbirds (*Trochilus polytmus*) were observed visiting *P. penduliflora* flowers between 1730 and 1900 h on the afternoon the flowers first opened but they were never observed visiting the same flowers in the morning. These hummingbird visits in the early evening were frequent with as many as 6 visits in 30 minutes. A total of 19 hummingbird visits to individual open flowers were recorded over six days. The hummingbirds drank nectar from the flowers by perching on the peduncles for two to three seconds. Hummingbirds were not observed contacting either male or female reproductive parts during their visits to open flowers. Their long tongues allowed them to drink from the flowers in such a manner that their heads, usually the part of the body on which pollen is deposited on hummingbird-pollinated passionflowers (Snow 1982, Kay 1999), never touched the anthers or stigma lobes.

The most frequent crepuscular visitors to open flowers of *P. penduliflora* were small-bodied, dark bats identified by their relative size, shape, and color as Greater Antillean long-tongued bats *Monophyllus redmani* (Fig. 2a). This bat species is a phyllostomid restricted to the Greater Antilles and southern Bahamas (Baker *et al.* 1984, Nowak 1994). It is also a nectarivorous bat species in the subfamily Glossophaginae, like *G. soricina*, which pollinates *P. mucronata* and *T. ovalis* (Sazima & Sazima 1978, Buzato & Franco 1992, Nowak 1994). Bats in this subfamily have elongated snouts and extensible tongues covered with bristle like papillae (Fig. 2b; Nowak 1994). While *G. soricina* is known to feed on nectar, fruit, pollen, flower parts, and insects, the food habits of *M. redmani* are poorly known (Lemke 1984, Nowak 1994).

Between 0 and 11 bat visits were observed on an individual plant per night and 18 visits in total were recorded over six days. The mammals were observed in the area as soon as the sun had set, foraging from 1900 to 2100 h. Bats were always observed hovering, but never clinging to, the flowers. Their visits were quick, about 1 second or less per flower, and sometimes with as little as 1 to 15 minutes between visits. They rarely visited more than one open flower on the same vine. This is consistent with a system in which cross-pollination is needed to ensure seed set. *Monophyllus redmani* was the only bat caught in mist nets from which *P. penduliflora* pollen was removed (Table 1). Pollen samples obtained from the

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FIGURE 1. (a) *Passiflora penduliflora* habit. Note the inverted flowers and the unusually long peduncles; (b) Longitudinal section of a flower at the beginning of the male phase. Note the position of the anthers and stigmas; (c) View from below a flower in the female phase. At this point the perianth is completely open, the styles and filaments are fully extended outward, and the stamen and stigma lobes are all pointing below. (Illustrations by Barbara Alongi from Mason River slides [a & c] and live collection by author; no. 104 from Barbecue Bottom, Jamaica [b]).

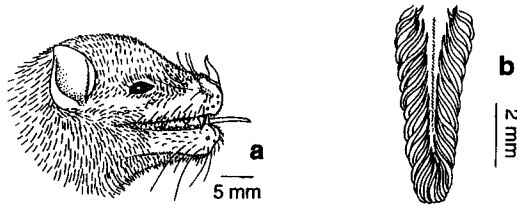


FIGURE 2. (a) Profile of the Greater Antillean long-tongued bat *Monophyllus redmani*; (b) Tongue of *M. redmani* with papillae. (Illustrations by Barbara Alongi from a Sam Noble Oklahoma Museum of Natural History specimen).

three *M. redmani* bats mist-netted showed 2, 46, and more than 300 grains of *P. penduliflora* present, respectively.

The time and manner in which *P. penduliflora* flowers are presented to visitors, the musty smell they release, and the secretion of dilute nectar at night is consistent with a bat-pollination syndrome (Faegri & Van Der Pijl 1976). *Passiflora penduliflora* also shares aspects of floral evolution with the two other bat-pollinated passionflowers, *P. mucronata* and *T. ovalis*, such as the production of copious pollen and deposition of this pollen between and behind the bat's ears (Sazima & Sazima 1978, Buzato & Franco 1992). Based on these observations, *M. redmani* is the most likely primary pollinator of *P. penduliflora* at this location.

The importance of hummingbirds as potential pollinators, however, should not be overlooked given that there is a window of time when open flowers and nectar are available for hummingbird visitors. More observations, pollinator exclusion experiments, and removal of pollen from hummingbirds are needed because there are examples of plant species having floral features that are intermediate between bat- and hummingbird-pollination syndromes (Buzato *et al.* 1994, Sazima *et al.* 1994). Detailed data on the pollination ecology of *P. penduliflora* is especially needed since this species is a good candidate sister species for the hummingbird-pollinated *P. perfoliata* from the dry forests of Jamaica. This relationship is supported by the shared distribution and unusual open bud development pattern found only in these two species within the Passifloraceae (Killip 1938; MacDougal 1994; Kay, pers. obs.). The relationship between the likely bat-pollinated *P. penduliflora* and the hummingbird-pollinated *P. perfoliata* may provide a future model system for studying the evolution of characters involved in pollinator shifts.

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TABLE 1. Number of bat species mist-netted near *Passiflora penduliflora* blossoms over two evenings at Mason River, Jamaica, and pollen types removed from them (July 1999). C = Convolvulaceae-type pollen; Pp = *P. penduliflora* pollen; and UM = Unknown monosulcate pollen.

Bat species mist-netted	Number of individuals	Number of individuals and their pollen types:		
		C	Pp	UM
<i>Artibeus jamaicensis</i>	2	0	0	0
<i>Artibeus flavescens</i>	2	0	0	0
<i>Monophyllus redmani</i>	3	3	3	3

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Using Artificial Fruits to Evaluate Fruit Selection by Birds in the Field¹

Key words: artificial fruits; Brazil; frugivory by birds; fruit color; fruit selection; semi-deciduous Atlantic forest.

THE PREFERENCE OF BIRDS FOR SPECIFIC FRUIT TRAITS has important implications for the evolution of bird behavior and fruit traits. Among the traits known to influence fruit choice are fruit color, size, accessibility, chemical characteristics, infructescence type, crop size, habitat, and distance between fruiting plants (Moore & Willson 1982, Levey *et al.* 1984, Denslow 1987, Sallabanks 1993, Fuentes 1994, Whelan &

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