Plant Syst Evol (2009) 281:247–250
DOI 10.1007/s00606-009-0193-5

SHORT COMMUNICATION

A presumed case of functional convergence between the flowers of *Schizolobium parahyba* (Fabaceae) and species of Malpighiaceae

I. Sazima · Mardiore Pinheiro · Marlies Sazima

Received: 18 August 2008 / Accepted: 18 May 2009 / Published online: 4 June 2009

Abstract Flowers of Malpighiaceae have a flag petal with a sturdy base that Centridini bees clasp with their mandibles to free their legs and thus be able to harvest oil. We found that the yellow, nectariferous flowers of *Schizolobium parahyba* (Fabaceae) have a forward-flexed upper petal with a sturdy claw and an adnate filament. Two *Centris* species were among the most frequent bee visitors to *S. parahyba* flowers. These bees clasped the adnate filament and the claw of the upper petal with their mandibles and extended their mouthparts into the corolla to take nectar. During the visit they leaned on, or loosely grabbed, the stamens. Blooming in the same area and period were two yellow-flowered *Stigmaphyllon* species (Malpighiaceae) whose pollen was also found on loads carried by the *Centris* bees. The flexion and the sturdiness of the upper petal claw of *Schizolobium parahyba* flowers may be viewed as a trait that suits the mandible clasp of *Centris* bees. Although this clasp is not needed when the bees visit *S. parahyba* flowers, it is vital when the bees exploit flowers of the Malpighiaceae. We suggest that the sturdy claw and the adnate filament of *S. parahyba* may be viewed as an instance of presumed functional convergence with the upper petal of Malpighiaceae.

I. Sazima
Museu de Zoologia, Instituto de Biologia, CP 6109,
Universidade Estadual de Campinas,
Campinas 13083-970, SP, Brazil

M. Pinheiro · M. Sazima (✉)
Departamento de Biologia Vegetal, Instituto de Biologia,
CP 6109, Universidade Estadual de Campinas,
Campinas 13083-970, SP, Brazil
e-mail: msazima@unicamp.br

Keywords *Schizolobium parahyba* · Floral features · *Centris* bees · Visiting behaviour · *Stigmaphyllon ciliatum* · *Stigmaphyllon arenicola* · Functional convergence

Introduction

The flag petal of the flowers in several species of Caesalpinioideae has a well-developed claw (Cowan 1981). This claw is found, e.g. in the genera *Bussea*, *Caesalpinia*, *Cenostigma*, *Hoffmannseggia*, *Parkinsonia*, *Peltophorum* and *Schizolobium* (Caesalpinieae); *Tylosema* = *Bauhinia* (Cercideae); and *Dicymbe* (Detarieae) (Cowan 1981; Cowan and Polhill 1981; Bortoluzzi 2004). In some melittophilous species of *Caesalpinia*, *Hoffmannseggia* and *Parkinsonia*, access to the nectar chamber is prevented by the claw and filaments and, thus, legitimate visitors (pollinators) have to insert their head and/or mouthparts between the upper petal and the androecial-gynoecium set to reach the nectar (Cocucci et al. 1992).

The flowers of American species of Malpighiaceae bear flag petals with a sturdy base that Centridini bees clasp to be able to free their specialised legs to harvest oil from the glands situated on the calyx (Vogel 1974). While on the flower, these specialised oil-gathering bees scrape the surface of the glands with their fore and middle legs to release and collect the oil (Vogel 1974, 1990; Sazima and Sazima 1989).

In a study of pollination biology of the fabaceous tree *Schizolobium parahyba* (Vell.) Blake, we noticed that Centridini bees landed on the flowers and clasped the adnate filament and the sturdy claw of the flexed upper petal. This behaviour would be unexpected as the bees took nectar only and thus had no need to free their legs. Additionally, we found two species of Malpighiaceae with

showy yellow flowers in bloom in the same area and period as *S. parahyba*. Here we briefly describe the flower of *S. parahyba*, the visiting behaviour of the Centridini bees, and comment on the possibility that the adnate filament and the sturdy claw of the flexed upper petal of *S. parahyba* may be viewed as an instance of presumed functional convergence with the flag petal of Malpighiaceae.

Materials and methods

The study site is in the coastal lowlands covered by sub-humid evergreen broadleaf forest, i.e. Atlantic rain forest (Eiten 1970; Sazima et al. 2003), at Picinguaba (about 23°20′S, 44°52′W) in Ubatuba, São Paulo, south-eastern Brazil. The canopy trees of *Schizolobium parahyba* were up to 40 m tall, and to reach the crown of two studied trees we stood on two scaffoldings 12 and 15 m high. Fieldwork was conducted in September 2006 (austral spring) over the course of 2 weeks. Number of flowers per inflorescences was recorded in situ, and floral morphology was examined in situ and in the laboratory. Frequency of visitors was determined by counting visits to about 25 flowers of different inflorescences over a total of 20 h on two non-consecutive days from 0700 to 1700 h. Behaviour of visitors was observed directly and photographed for further analyses of their behaviour. "Ad libitum" and "behaviour" sampling rules (Martin and Bateson 1986), the former for preliminary observations and the latter for each occurrence of a particular type of behaviour (together with details on the involved individuals), were used throughout the observations. Flowers were examined under a stereomicroscope to check for scars in the claw of the upper petal caused by Centridini bees. Pollen loads from the scopae and ventral side of abdomen and thorax of female *Centris labrosa* Friese ($n = 3$) and *Centris varia* (Erichson) ($n = 3$) caught at flowers of *Schizolobium parahyba* were compared with pollen samples of *S. parahyba* and two synchronopatric *Stigmaphyllon* species, *S. arenicola* C. E. Anderson and *S. ciliatum* (Lam.) A. Juss. Voucher specimens of plants and floral visitors are deposited at the herbarium (UEC) and the insect collection of the Museu de Zoologia (ZUEC) of the Universidade Estadual de Campinas, São Paulo.

Results

The complex inflorescences (compound racemes) of *Schizolobium parahyba* are held erect above the crown foliage. The total number of inflorescences on a 30-m-tall tree was 1,035 with a total of 9,315 racemes. With an average of 40 (range 11–76) flowers per raceme, this tree produced about 370,000 flowers during its blooming. The diameter of the flowers was 34.7 mm ± 2.3 ($n = 15$). The dialipetalous corolla is composed of bright yellow petals, the flexed upper one upright with a sturdy claw (3.7 × 1.4 mm, $n = 15$), and four showy lateral petals. The flower has 10 stamens, one upright and adnate with the upper petal (Fig. 1c), and the others at about 90° facing this petal. The pistil and these stamens form the androecial-gynoecium set. The nectar is hidden in the nectar chamber.

Medium to large bees were the main visitors to *S. parahyba* flowers. The Centridini bee *Centris labrosa* was the most frequent visitor (Table 1). *Centris varia*, *Xylocopa frontalis* (Olivier), and *Megachile* spp. were less frequent but also important visitors (Table 1). The Centridini bees visited the flowers for nectar only. These bees landed on the centre of the flower (Fig. 1a), clasped the base of the sturdy upright filament and the claw of the upper petal with their mandibles, and introduced the mouthparts at the petal base and that of the androecial-gynoecium set, thus reaching the nectar chamber (Fig. 1b). While on the flower, the bees did not use their legs to hold position and they only leaned on, or loosely grabbed, the androecial-gynoecium set, thus touching the anthers and stigmas. The examined claws of the upper petal of *S. parahyba* showed light depression marks made by the Centridini bees during their visit to the flower (evidence of the bees' clasp on this floral part). Only centridine bees clasped the claw of the upper petal of *S. parahyba*, the other bee species either landed on the flower or grasped flower parts other than the above-mentioned claw to take nectar or gather pollen.

We found two Malpighiaceae species, *Stigmaphyllon ciliatum* and *S. arenicola* (Fig. 1d), with showy yellow flowers blooming in the study area at the same time as *Schizolobium parahyba.* The diameter of the flowers for the two former species was 31.7 mm ± 1.4 ($n = 10$) and 24.5 mm ± 1.4 ($n = 15$), respectively. Up to 300–400 flowers could be found open at a time on each of the *Stigmaphyllon* species, particularly the fully grown plants. These are lianas that climb up shrubs and trees in the Atlantic forest, and thus are accessible to Centridini bees in the same period and level they visit *S. parahyba*. Pollen loads taken from the females of the two species of *Centris* yielded mostly *Schizolobium parahyba* pollen; *Stigmaphyllon* spp. (including *S. ciliatum* and *S. arenicola*) pollen was found as well, albeit in smaller amounts.

Discussion

A modified upper petal is widespread in the Caesalpinioideae (Cowan 1981), and the primary function of the well-developed claw and filaments in some species is allegedly

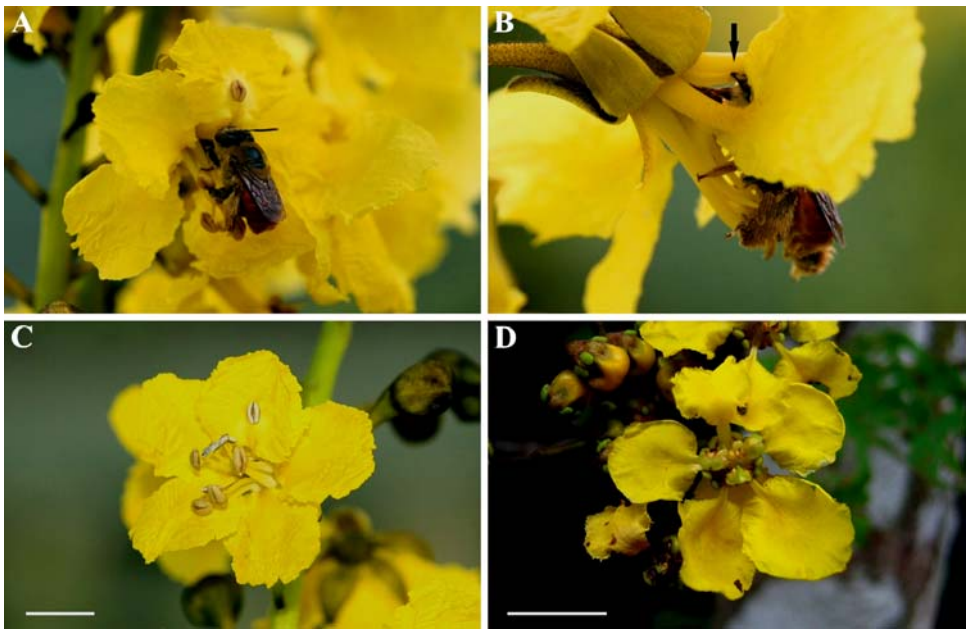

Fig. 1 Visits of centridine bees *Centris labrosa* (females) on flowers of the caesalpinioid *Schizolobium parahyba*, and a flower of the latter plus a synchronopatric species of Malpighiaceae in frontal views. **a** Flower of *Schizolobium parahyba* showing the upper petal curved forward, the adnate filament, and the fit between the bee's size and posture with the arrangement of the flower's stamens and stigma. **b** Lateral view of the bee on a flower, showing the mandible clasp (*arrow*) on the adnate filament and the claw of the upper petal while taking nectar with extended mouthparts. **c** Flowers of *Schizolobium parahyba* (Fabaceae) and **d** *Stigmaphyllon arenicola* (Malpighiaceae) showing their overall similarity including wrinkled petals with indented margins. *Scale bars* 10 mm

Table 1 Main bee visitors and their visiting frequency to flowers of *Schizolobium parahyba* (20 h over two non-consecutive days) at the Parque Estadual da Serra do Mar, Ubatuba, São Paulo, south-eastern Brazil

Flower visitors	Number and percentage of visits
Apidae	
Centris (*Heterocentris*) *labrosa*	553 (31%)
Centris (*Centris*) *varia*	245 (14%)
Xylocopa (*Megaxylocopa*) *frontalis*	296 (16%)
Megachilidae	
Megachile sp. 1	425 (24%)
Megachile sp. 2	176 (10%)
Megachile sp. 3	92 (5%)

the prevention of free access to the nectar chamber (Cocucci et al. 1992). In the particular instance we recorded for *Schizolobium parahyba*, this floral part acquires an important secondary function, i.e. a structure for the Centridini bees to clasp while visiting the flowers to take nectar. As centridine bees behave similarly on the flowers of Malpighiaceae to free their legs and be able to harvest oil (Vogel 1974, 1990; Sazima and Sazima 1989), we surmise that their clasping the base of the sturdy claw and the upright filament of the upper petal of *S. parahyba* flower may be viewed as an instance of fixed or stereotyped behaviour, since the bees have no need to free their legs to take nectar. This being the case, we predict that Centridini bees would clasp the claw of the modified upper petal of other caesalpinioid genera such as *Bussea*, *Caesalpinia*, *Cenostigma*, *Dicymbe*, *Hoffmannseggia*, *Parkinsonia*, *Peltophorum*, and *Tylosema*, species of which occur in South America (Cowan 1981; Cowan and Polhill 1981; Bortoluzzi 2004).

The sturdy claw and the upright filament of the upper petal of *S. parahyba* are morphological traits that may be viewed as an instance of presumed functional convergence with the flag petal of the Malpighiaceae. The pollen loads support the view that centridine bees do visit flowers of *Schizolobium parahyba* and *Stigmaphyllon* spp. in the course of their daily foraging bouts. The overall similarity in colour, form and size between the flowers of *S. parahyba* and the two synchronopatric species of Malpighiaceae raises the possibility that this Fabaceae mimics the flowers of the latter, however speculative this view may seem. An opposite view, i.e. that the similarity is entirely fortuitous, cannot be ruled out, but instances of functional convergence and mimicry among flowers are widespread (e.g. Vogel 1994; Endress 1994), and thus our suggestion is deemed acceptable from a pollination biology perspective.

Acknowledgments We thank the Instituto Florestal (Parque Estadual da Serra do Mar, Núcleo Picinguaba) for the permit to study pollination biology of Fabaceae on protected public lands, and

Adriano Kid Azambuja and Rubem Samuel de Ávila Jr. for valuable help in the field. M.P. had a grant from the FAPESP, and I.S. and M.S. have research grants from the CNPq. This research was partially supported by the State of São Paulo Research Foundation (FAPESP) as part of the Thematic Project Functional Gradient (Process Number 03/12595-7), within the BIOTA/FAPESP Program—The Biodiversity Virtual Institute (http://www.biota.org.br). COTEC/IF 41.065/2005 and IBAMA/CGEN 093/2005 permits.

References

Bortoluzzi RLC (2004) A subfamília Caesalpinioideae (Leguminosae) no estado de Santa Catarina, Brasil. Ph.D. Thesis, Universidade Federal do Rio Grande do Sul, Brasil

Cocucci AA, Galetto L, Sérsic A (1992) El síndrome floral de *Caesalpinia gilliesii* (Fabaceae-Caesalpinioideae). Darwiniana 31:111–135

Cowan RS (1981) Caesalpinioideae. In: Polhill RM, Raven PH (eds) Advances in legume systematics. Royal Botanic Gardens, Kew, pp 57–64

Cowan RS, Polhill RM (1981) Detarieae. In: Polhill RM, Raven PH (eds) Advances in legume systematics. Royal Botanic Gardens, Kew, pp 117–134

Eiten G (1970) A vegetação do Estado de São Paulo. Bol Inst Bot 7:1–147

Endress PK (1994) Diversity and evolutionary biology of tropical flowers. Cambridge University Press, Cambridge

Martin P, Bateson P (1986) Measuring behaviour, an introductory guide. Cambridge University Press, Cambridge

Sazima M, Sazima I (1989) Oil-gathering bees visit flowers of eglandular morphs of the oil-producing Malpighiaceae. Bot Acta 102:106–111

Sazima M, Buzato S, Sazima I (2003) *Dyssochroma viridiflorum* (Solanaceae): a reproductively bat-dependent epiphyte from the Atlantic Rainforest in Brazil. Ann Bot 92:725–730

Vogel S (1974) Ölblumen und ölsammelnde Bienen. Trop Subtrop Pflanzenwelt 7:283–547

Vogel S (1990) History of the Malpighiaceae in the light of pollination ecology. Mem NY Bot Gard 55:130–142

Vogel S (1994) Radiación adaptativa del síndrome floral en las familias neotropicales. Bol Acad Nac Cienc Córdoba 59:5–30