

Stamen movements in flowers of *Opuntia* (Cactaceae) favour oligolectic pollinators

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Abstract: *Opuntia brunneogemmia* and *O. viridirubra* occur sympatrically in the Serra do Sudeste, Rio Grande do Sul, Brazil. Their flowers have 450–600 thigmonastic stamens and provide large amounts of pollen and nectar for bees. Bees of 41 species were registered at the flowers of *O. brunneogemmia* and 30 at the flowers of *O. viridirubra*. Females of three oligolectic species are the only effective pollinators: *Ptilothrix fructifera* (*Anthophoridae*), *Lithurgus rufiventris* (*Megachilidae*), and *Cephalocolletes rugata* (*Colletidae*). During their visits in *Opuntia*-flowers, bees touch the filaments and stimulate the movement of the stamens to the centre of the flower. At the end of this movement, the anthers are densely packed around the style. As a consequence the pollen is presented in an easily accessible upper layer of anthers and various, nearly inaccessible lower layers. The lower layers contain about 80% of the pollen reward. Only females of the three oligolectic pollinators exploit the pollen from the lower layers and reach the nectar furrow. Therefore, through their stamen movements, *Opuntia* flowers hide most of their pollen from flower visitors but favour effectively pollinating, oligolectic bees.

The distribution of the genus *Opuntia* stretches from Canada to Patagonia. It comprises cacti which grow as small trees, shrubs and dwarf cushions (HUNT 1989, BARTHOLOTT & HUNT 1993). Information to the pollination biology of South American opuntia cacti are scarce. Studies on the *Opuntia* species in North America have shown that their flowers are pollinated by polylectic as well as oligolectic bees (GRANT & GRANT 1979a, b; GRANT & HURD 1979; GRANT & al. 1979; SPEARS 1987; OSBORN & al. 1988; MCFARLAND & al. 1989).

The flowers of *Opuntia brunneogemmia* (RITTER) SCHLINDWEIN and *O. viridirubra* (RITTER) SCHLINDWEIN are cup-shaped and have 450–600 sensitive stamens, a common feature among *Opuntia* species (PORSCH 1938, RAUH 1979). After mechanical stimulation, the stamens move toward the style and after some minutes bend outwards again (Fig. 1). Like in other *Opuntia* species, the pollen grains are very large, measuring up to 150 µm in diameter (LEUENBERGER 1976, SCHLINDWEIN 1995). Nectar is produced in a groove at the base of the style. During the summer (November to January), opuntia cacti are in mass flowering, while other plants in

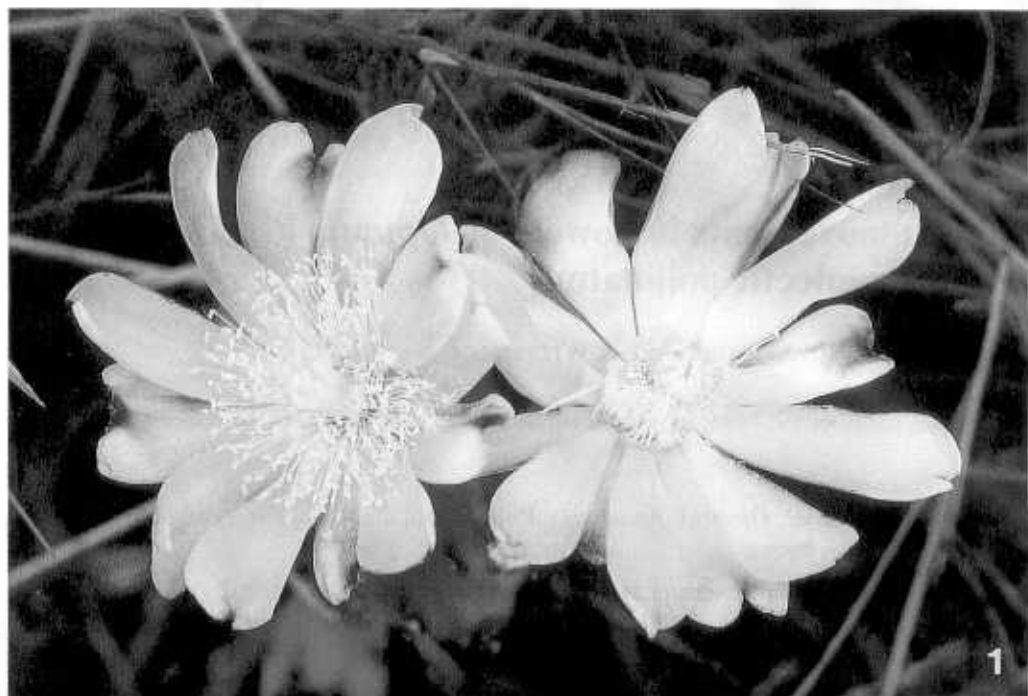


Fig. 1. Flowers of *Opuntia viridirubra*. The stamens of the right flower were stimulated and moved to the centre of the flower. – Fig. 2. A female of *Ptilothrix fructifera* in a flower of *Opuntia brunneogemma*. After alighting on the stigma, she pushes her body downwards, pressing her stiff hind tibial spurs and hind tarsi against the protruding head of the stigma

their habitats produce few flowers. Therefore, it could be expected that bees of many species collect floral resources on these rich pollen and nectar resources. The large size of the *Opuntia* pollen grains, however, should favour morphologically adapted bees with a specialised scopa to transport the pollen.

It can be presumed that stamen movements play a role in the pollination of *Opuntia* flowers. While TROLL (1992) in general did not admit functional interpretations of stamen movements, VOGEL (1983) emphasised their function in floral biology to promote outbreeding. RAUH (1979) suggested that stamen movements in *Opuntia* facilitate the deposition of pollen grains on the body of the visiting insect, while PORSCH (1938) suggested that they cause insects to depart from the stigma. GRANT & HURD (1979) pointed out that this would only promote self-pollination.

The aim of the present study was to determine (a) the flower visiting bees of *Opuntia brunneogemmia* and of *O. viridirubra*, (b) which of these bees are effective pollinators and (c) the function of stamen movements for pollination of *Opuntia* flowers.

Material and methods

Study sites. The field study was carried out from October to February 1991–1994 in the region of the Guaritas, (districts Caçapava do Sul, Lavras do Sul and Santana da Boa Vista) in the Serra do Sudeste, Rio Grande do Sul, Brazil. The location where most observations and experiments were made is at 30° 48' 06" S, 53° 26' 15" W. The Guaritas (watchtowers) are steep, 30–60 m high blocks of Cambrian-Ordovician sandstones and conglomerates which bear a sparse vegetation. Dominant are xerophytic scrub formations which are intermingled with semi-natural grasslands. *Opuntia* habitats are sun exposed, rocky slopes and areas with little developed soils under pastures.

The climate is subtropical to temperate and humid almost throughout the year. Mean annual rainfall is 1400 mm. Drought can occur in summer. Days with frost are frequent in July and August, while the mean temperature maximum in January is 31°C (OLIVEIRA & RIBEIRO 1986).

***Opuntia* species.** *Opuntia brunneogemmia* (described as *Platyopuntia brunneogemmia* RITTER; RITTER 1979: 34, 35) is a robust shrub reaching a height of up to 1.5 m. Flower buds are pointed apically and petals are intensely orange coloured. Floral length including ovary is 75–95 mm, floral width is 60–80 mm and style length including the 7–8 stigma lobes is 26–31 mm. *Opuntia viridirubra* was described as *Platyopuntia viridirubra* RITTER and *P. rubrogemmia* RITTER (RITTER 1979: 33–36); both *Platyopuntia* species are transferred to *Opuntia* in SCHLINDWEIN & WITTMANN (1995: 29). Plants of *O. viridirubra* are generally smaller (up to 1 m height). Flower buds are rounded apically and petals are orange to yellow coloured. Floral length including ovary is 65–85 mm, floral width is 59–72 mm and style length including the 9–10 stigma lobes is 22–27 mm. Flowers of both species have a nectar groove at the base of the style. The stigma lobes are receptive at their outer surfaces. The size of the pollen grains of *O. brunneogemmia* ranges from 86–150 µm, those of *O. viridirubra* from 88.5–128 µm (SCHLINDWEIN 1995). An adult plant of each *Opuntia* species might bear up to 200 blossoms, from which more than ten may be open at the same day at peak of flowering. Both *Opuntia* species are endemic to southern Rio Grande do Sul. In the Guarita region, they are the only known *Opuntia* species. Nowadays they are abundant due to extensive stock farming.

Compatibility systems. 30 flower buds of each *Opuntia* species were bagged with paper pouches. At anthesis, 10 flowers of each species were self-pollinated by hand, 10 cross

pollinated by hand and the remaining 10 flowers were not treated and kept bagged as controls. A further 20 flowers of both *Opuntia* species were marked and used as open pollinated controls. These flowers were visited by bees and pollen was deposited on the stigma. Seeds were counted from all mature fruits.

Survey of bees at *Opuntia* flowers. Voucher specimens of bees were collected in the *Opuntia* flowers. Furthermore, bees were captured at flowers of other plants at the study sites to check which of the cactus visiting bees also collect nectar or pollen from non-*Opuntia* species. Specimens of bees and plants are kept in the bee collection and the herbarium of the Biological Research Station of the University of Tübingen (Germany) at the Biological Institute of the PUC-RS (Pontifícia Universidade Católica do Rio Grande do Sul) in Porto Alegre (Brazil).

When only the generic name of a bee is given, the species is either not yet described or it was not possible to identify the individual to species level. In these cases, the species numbers refer to those used in the bee collection of the Biological Research Station.

Frequencies of bees in *Opuntia* flowers and stigma contacts. The frequencies of visits by bees to the flowers of *Opuntia brunneogemma* were determined by counting female and male bees during a total of 42 hours of observation, those of *O. viridirubra* during a total of 38 hours of observation. During each visit we checked whether the bees came into contact with the stigma. The relative frequencies of stigma contacts were calculated for males and females of each bee species.

Analyses of pollen loads. Ten females of each bee species were captured at flowers of both *Opuntia* species. Their pollen loads were stripped off the scopa and some drops of 70% ethanol were added. The pollen grains were mixed, picked up on a small piece of glycerine gelatine and transferred to a microscope slide. The glycerine gelatine was melted gently, mounted with a cover glass and sealed with paraffin wax. Two samples were made of each pollen load, with pure glycerine gelatine and with glycerine gelatine stained with alcoholic fuchsin solution. Pollen loads were analysed by counting at least 200 pollen grains per sample. Pollen was identified by comparison with a pollen reference collection of the study area. The relative abundance of *Opuntia* pollen in the scopal loads was taken to quantify the flower fidelity of the bees.

Evaluation of *Opuntia* pollinators. The efficiency of the bees as pollinators of the *Opuntia* flowers was determined by evaluating the combination of "relative frequency of stigma contacts" and "flower constancy", complemented by observations on the flight routes between conspecific flowers.

Function of the stamen movements. The behaviour of the bees during flower visits was analysed from video recordings (Panasonic F10 Mark II video camera equipped with a 100 mm macro lens). Their behaviour in flowers in which stamens had been stimulated due to former bee visits was compared with those in flowers with unstimulated stamens.

Results

The flowering period of both *Opuntia* species extends from mid-spring to mid-summer. Flowering plants of *O. brunneogemma* were recorded from 26 Oct. to 20 Febr., those of *O. viridirubra* from 27 Oct. to 16 Febr.

Anthesis. The anthesis of *O. brunneogemma* flowers lasts for six to eight hours. Flowers open any time of the day between 8:00 h and 15:00 h. Flowers which open during the morning until noon close between 14:30 h and 18:00 h and do not open again on subsequent days. Flowers which open in the afternoon close at about 18:00 h and generally, for a few hours, open again on the subsequent morning until they reach a total period of anthesis of six to eight hours. Pollen is presented at the

Table 1. Compatibility and seed set of the flowers of *Opuntia brunneogemma* and *O. viridirubra*. n number of flowers examined, \bar{x} average, s standard deviation

| Flowers | n | <i>Opuntia brunneogemma</i> | | <i>Opuntia viridirubra</i> | |
|---------------------------|----|-----------------------------|------|----------------------------|------|
| | | \bar{x} | s | \bar{x} | s |
| Bagged (not treated) | 10 | 1.1 | 2.2 | 6.8 | 8.5 |
| Hand self-pollinated | 10 | 29.0 | 16.6 | 30.5 | 13.1 |
| Hand cross-pollinated | 10 | 46.3 | 24.7 | 60.8 | 15.0 |
| Open pollinated (control) | 20 | 55.2 | 25.8 | 63.7 | 16.5 |

beginning of anthesis. When the petals diverge and permit the first flower visits, all anthers are already dehiscent. The characteristics of anthesis of *O. viridirubra* coincide with those described for *O. brunneogemma*, with the difference that anthesis lasts for 6 to 12 hours.

Auto-compatibility and seed set. The flowers of both *Opuntia* species are moderately autocompatible (Table 1). Flowers self-pollinated by hand produce about half of the seeds of bee-pollinated flowers. Seed set of flowers cross-pollinated by hand is similar to that of bee-pollinated flowers. Permanently bagged flowers of both species set almost no seed.

Frequencies and stigma contacts of flower visiting bees. During 42 hours observation time we counted 1172 visits by bees in flowers of *O. brunneogemma* and, during 38 hours, 801 visits in flowers of *O. viridirubra*. Bees of 48 species from six families were recorded in the *Opuntia* flowers, 41 species in the flowers of *O. brunneogemma* and 30 in the flowers of *O. viridirubra* (Table 2). The smallest flower visiting bees are workers of the stingless bee *Plebeia wittmanni* (3.5 mm) and the largest are females of the carpenter bee *Xylocopa frontalis* (25–30 mm).

Table 2. Flower-visiting bees of *Opuntia brunneogemma* and *O. viridirubra*

| Bee species | <i>O. brunneogemma</i> | <i>O. viridirubra</i> |
|---|------------------------|-----------------------|
| Andrenidae | | |
| <i>Anthrenoides micans</i> URBAN | | ♀, ♂ |
| <i>Arhysosage cactorum</i> MOURE | ♀, ♂ | ♀, ♂ |
| <i>Callonychium petuniae</i> CURE & WITTMANN | ♀, ♂ | |
| <i>Panurgillus</i> sp. | ♀ | |
| Anthophoridae | | |
| <i>Alloscirtetica (Dasyscirtetica) gilva</i> (HOLMBERG) | ♀, ♂ | ♀ |
| <i>Ancyloscelis fiebrigi</i> (BRÈTHES) | ♀, ♂ | ♀, ♂ |
| <i>Centris (Paracentris) tricolor</i> (FRIESE) | ♂ | ♂ |
| <i>Ceratina ischiocentra</i> MOURE | | ♀ |

Table 2 (continued)

| Bee species | <i>O. brunneogemma</i> | <i>O. viridivirbra</i> |
|--|------------------------|------------------------|
| <i>Ceratina morrensis</i> STRAND | ♀ | |
| <i>Ceratina (Crewella) asuncionis</i> STRAND | ♀ | |
| <i>Ceratina (Crewella) rupestris</i> HOLMBERG | ♀ | |
| <i>Ceratina (Rhyzoceratina) hyemalis</i> MOURE | ♀ | |
| <i>Lanthanomelissa (Lanthanella) completa</i> MICHENER & MOURE | ♀ | |
| <i>Melissoptila (Ptilomelissa) bonaerensis</i> HOLMBERG | ♀ | |
| <i>Ptilothrix fructifera</i> (HOLMBERG) | ♀, ♂ | ♀, ♂ |
| <i>Tapinotaspis sabularum</i> HOLMBERG | ♀ | ♀ |
| <i>Tetrapedia rugulosa</i> FRIESE | ♀ | ♀ |
| <i>Xylcopa (Neoxylcopa) augusti</i> LEPELETIER | ♀ | |
| <i>Xylcopa (Megaxylcopa) frontalis</i> (OLIVIER) | ♀ | |
| Apidae | | |
| <i>Apis mellifera</i> L. | ♀ | |
| <i>Bombus (Fervidobombus) atratus</i> FRANKLIN | ♀ | |
| <i>Mourella caerulea</i> (FRIESE) | ♀ | |
| <i>Plebeia emerina</i> (FRIESE) | ♀ | |
| <i>Plebeia wittmanni</i> MOURE & CAMARGO | ♀ | ♀ |
| <i>Trigona spinipes</i> (FABRICIUS) | ♀ | ♀ |
| Colletidae | | |
| <i>Cephalocolletes rugata</i> URBAN | ♀ | ♀ |
| <i>Sarocolletes</i> sp. 3 | ♀ | ♀ |
| Halictidae | | |
| <i>Augochlora (Augochlora) amphitrite</i> (SCHROTTKY) | ♀ | ♀ |
| <i>Augochlora (Augochlora) daphnis</i> SMITH | ♀ | ♀ |
| <i>Augochlora (Augochlora)</i> sp. 6 | ♀ | ♀ |
| <i>Augochlora (Augochlora)</i> sp. 7 | ♀ | |
| <i>Augochlora (Augochlora)</i> sp. 8 | | ♀ |
| <i>Augochlora (Oxystoglossella) semiramis</i> (SCHROTTKY) | ♀ | |
| <i>Augochlorella michaelis</i> (VACHAL) | ♀ | |
| <i>Augochloropsis cupreola</i> (COCKERELL) | ♀ | |
| <i>Augochloropsis euterpe</i> (HOLMBERG) | ♀ | ♀ |
| <i>Augochloropsis</i> sp. 8 | ♀ | |
| <i>Dialictus (Chloralictus) opacus</i> (MOURE) | ♀ | |
| <i>Dialictus (Chloralictus)</i> sp. | ♀ | ♀ |
| <i>Dialictus (Dialictus)</i> sp. | | ♀ |
| <i>Thectochlora alaris</i> (VACHAL) | ♀ | ♀ |
| Megachilidae | | |
| <i>Lithurgus pygmaeus</i> FRIESE | ♂ | |
| <i>Lithurgus rufiventris</i> FRIESE | ♀, ♂ | ♀, ♂ |
| <i>Megachile (Acentrina)</i> sp. | ♂ | |
| <i>Megachile (Chrysosarus) guaranitica</i> SCHROTTKY | | ♂ |
| <i>Megachile (Chrysosarus)</i> sp. | | ♀ |
| <i>Megachile (Leptorachis)</i> sp. | ♂ | |
| <i>Megachile (Pseudocentron)</i> sp. | ♀ | ♀ |

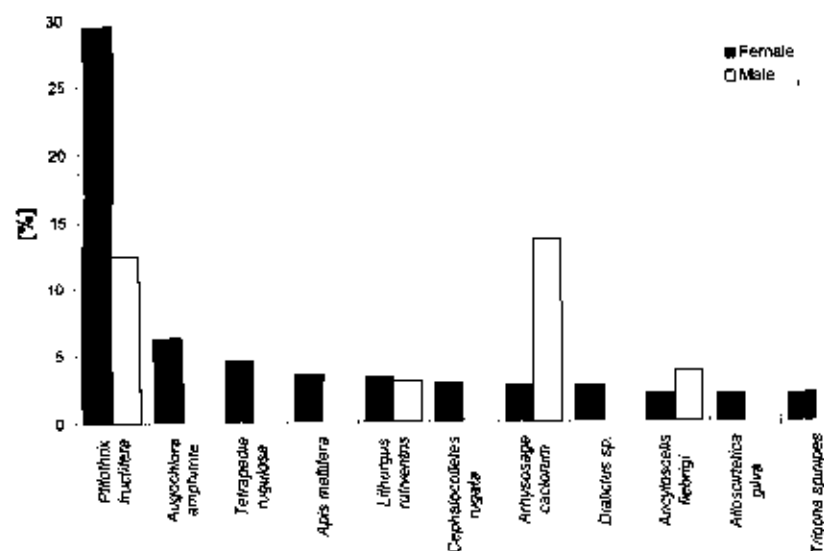


Fig. 3. Relative frequency of visits by bees to flowers of *Opuntia brunneogenmia* (n = 1172)

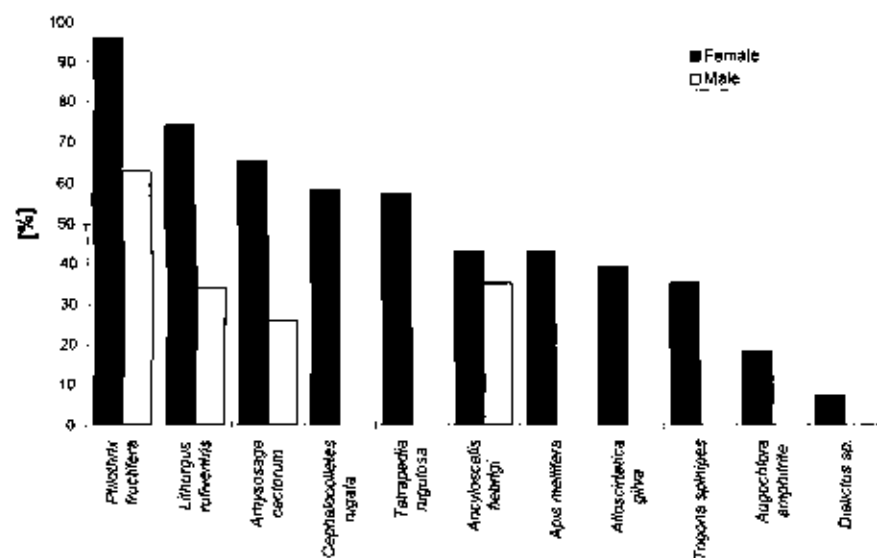


Fig. 4. Relative frequency of stigma contacts by bees in flowers of *Opuntia brunneogenmia*

Regular flower visitors (more than 1 visit per species in 2 hours of observation) were bees of 11 species at the flowers of *O. brunneogenmia* and 10 bee species at the flowers of *O. viridibrubra* (Figs. 3, 6). Among them, females of *Ptilothrix fructifera* are the most frequent flower visitors of both *Opuntia*-species. Bees which visited *Opuntia* flowers only sporadically (less than 1 visit per species in 2 hours of observation) are not treated further here.

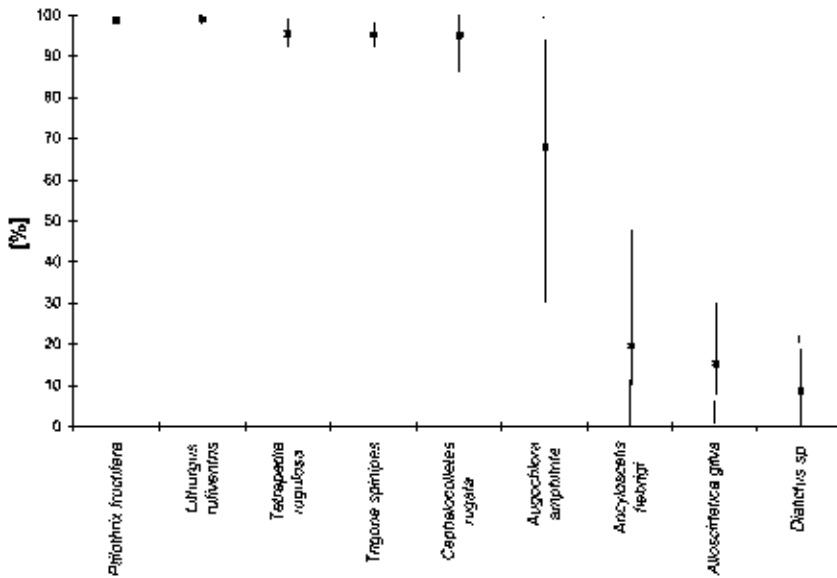


Fig. 5. Relative amount of pollen from *Opuntia brunneogemma* in the scopae of females (n = 10)

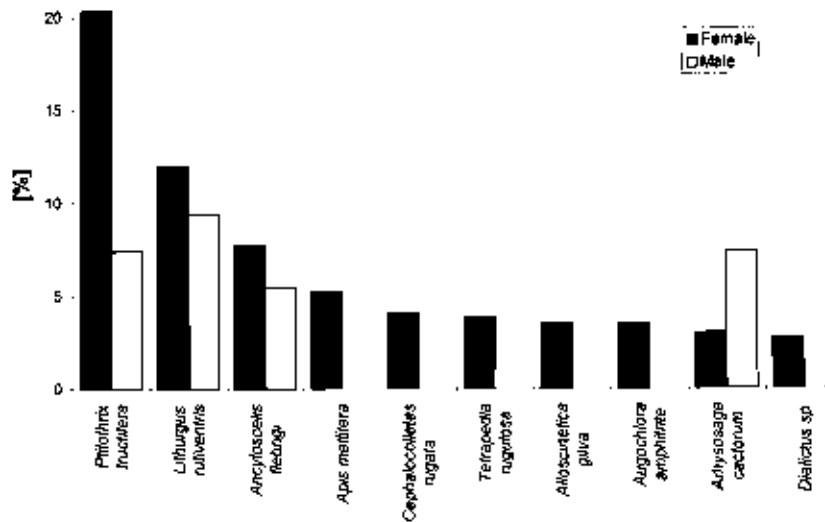


Fig. 6. Relative frequency of visits by bees to flowers of *Opuntia viridirubra* (n = 801)

Females of *Ptilothrix fructifera* touched the stigma during almost all visits to flowers of *O. brunneogemma* and *O. viridirubra* (Figs. 4, 7). They generally alight on the stigma and thus deposit pollen already at the beginning of their flower visits. Also females of *Lithurgus rufiventris*, *Cephalocolletes rugata*, *Tetrapedia rugulosa* and *Apis mellifera* frequently touched the stigma (Figs. 4, 7). Stigma contacts were rare during

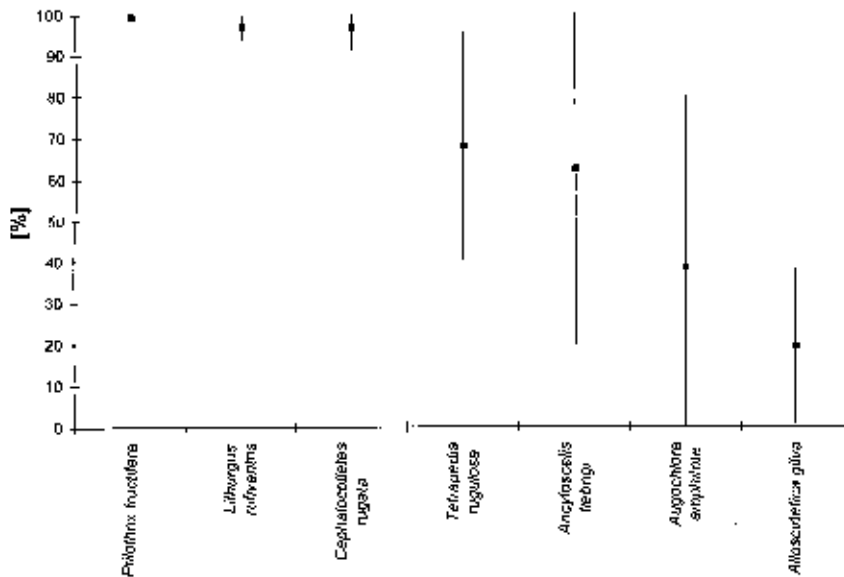


Fig. 8. Relative frequency of stigma contacts by bees in flowers of *Opuntia viridirubra*

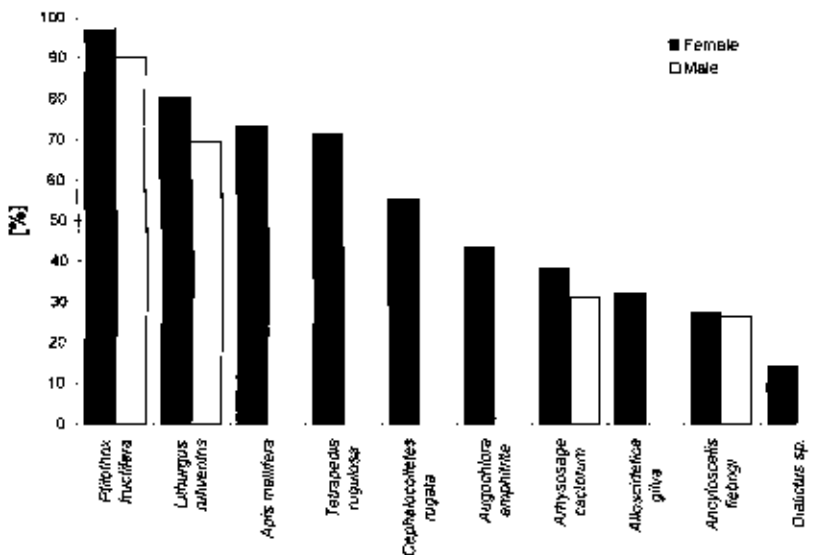


Fig. 7. Relative amount of pollen from *Opuntia viridirubra* in the scopae of females (n = 10)

flower visits of females of *Dialictus* sp. at both *Opuntia* cacti and of females of *Augochlora amphitrite* at the flowers of *O. brunneogemmia* (Figs. 4, 7).

Effective pollinators of *Opuntia*-flowers. Females of *Ptilothrix fructifera* and *Lithurgus rufiventris* are effective pollinators of both *Opuntia* species. They show flower fidelity (Figs. 5, 8), frequently touch the stigma (Figs. 4, 7) and move busily

Table 3. Bee visits at flowers, other than *Opuntia brunneogemmia* and *O. viridirubra*. Other opuntias are *O. monacantha* and *O. paraguayensis*; *Notocactaceae* are *Trialetia*, *Cyanocephalum* and *Notocactus*. + = frequent visits, - = few visits, - = no visits. * data exclusively from pollen analyses. ** pollinaria on frons of bee

| Bee species | Visits of females to flowers of | | |
|-------------------------------|---------------------------------|----------------------|---|
| | other opuntias | <i>Notocactaceae</i> | other plant families |
| <i>Allosectretica gilva</i> | | | numerous* |
| <i>Ancyloscelis fiebrigii</i> | | + - | <i>Convolvulus</i> , <i>Excochulus</i> *, <i>Ipomoea</i> , <i>Merremia</i> (<i>Convolvulaceae</i>) <i>Cuphea</i> (<i>Lythraceae</i>) |
| <i>Apis mellifera</i> | - | | numerous |
| <i>Arhysosage cactorum</i> | | ++ | |
| <i>Augochlora amphirrite</i> | + - | + | numerous |
| <i>Dialictus</i> sp. | + | ++ | numerous |
| <i>Lithurgus rufiventris</i> | | | |
| <i>Ptilothrix fructifera</i> | ++ | - | - |
| <i>Cephalocolletes rugata</i> | | ++ | <i>Monnina</i> (<i>Polygalaceae</i>) |
| <i>Tetrapedia rugulosa</i> | ++ | + | <i>Asteraceae</i> *, <i>Croton</i> (<i>Euphorbiaceae</i>)*, <i>Janusia</i> (<i>Malpighiaceae</i>)*, <i>Ludwigia</i> (<i>Onagraceae</i>), <i>Oncidium</i> (<i>Orchidaceae</i>)** |
| <i>Trigona spinipes</i> | - | + | numerous |

between flowers of different *Opuntia* individuals. The males of both species patrolled the *Opuntia* flowers in search of females, and the males of *Ptilothrix fructifera* used them as sleeping sites. Patrolling also results in pollination as males often visit flowers to take nectar and frequently touch the stigmas. Bees of both species were recorded throughout the flowering period of *Opuntia* species. Pollen analyses of seven brood cells of *Ptilothrix fructifera* confirmed the results of the analyses of the pollen loads. The brood cells contained between 99.5 and 100% pollen of the studied *Opuntia* species. Females and males of *Ptilothrix fructifera* were also frequent visitors of the flowers of *Opuntia monacantha* and *O. paraguayensis*, which are allopatric to *O. brunneogemmia* and *O. viridirubra* (Table 3).

Females of *Cephalocolletes rugata* are also most likely effective pollinators of both *Opuntia* species. The females, which have only a short flight period in spring, also intensely collected pollen from flowers of various *Notocactus* species (Table 3). Females of *Tetrapedia rugulosa* are also probably effective pollinators of *O. brunneogemmia*; they did not show fidelity to the flowers of *O. viridirubra* (Fig. 8) and thus might be only mediocre pollinators.

Worker bees of the highly eusocial *Apis mellifera* and *Trigona spinipes* were not effective pollinators of *Opuntia* flowers because individuals repeatedly visited the same flower, generally only of a single plant specimen. This behaviour only results in self-pollination. Hovering near *Opuntia* flowers, honey bees were observed to strip

off the large *Opuntia* pollen grains from their body. They visited the flowers in search for nectar.

Females of the other bees had mixed pollen loads. Females of *Alloscirtetica gilva*, *Ancyloscelis fiebrigi* and *Augochlora amphirrite* are pollinators of low effectiveness because of their low flower constancy and their low relative frequency of stigma contacts (Figs. 4-5, 7-8). Females of *Ancyloscelis fiebrigi* visited the *Opuntia* flowers mainly to collect nectar (Table 4). Non-*Opuntia* pollen came mainly from *Convolvulus* and *Eriofolius* (*Convolvulaceae*), which reached 63.7% on average in females caught in flowers of *O. brunneogemma*. Therefore, the content of *Opuntia* pollen was low in the scopal loads of these bees. Females of the solitary *Alloscirtetica gilva* always carried a mixture of four to eight pollen types in their scopae, among others from *Asteraceae*, *Euphorbiaceae*, *Lythaceae*, *Malvaceae* and *Rubiaceae*. Females of *Dialictus* sp. did not contribute to cross pollination. They rarely touched the stigma and showed little flower fidelity (Figs. 4, 5, 7).

Characteristics of the stamen movements. The flowers of *O. brunneogemma* have on average 598 stamens (standard deviation; $s = 49$; number of examined flowers, $n = 5$), the flowers of *O. viridicubra* 450 stamens ($s = 18$, $n = 5$). After a flower visiting bee mechanically stimulated the filaments, the stimulated stamens immediately bend inwards to the style (Fig. 1). The outer stamens, which insert at the rim of the concave flower tube, have long filaments. In the stimulated state, they cover the shorter inner stamens which insert at the bottom around the nectar groove (Fig. 9). This means, the *Opuntia* flowers offer their pollen in an upper and various lower layers of anthers. As a consequence, the pollen of the inner stamens is not freely accessible to flower

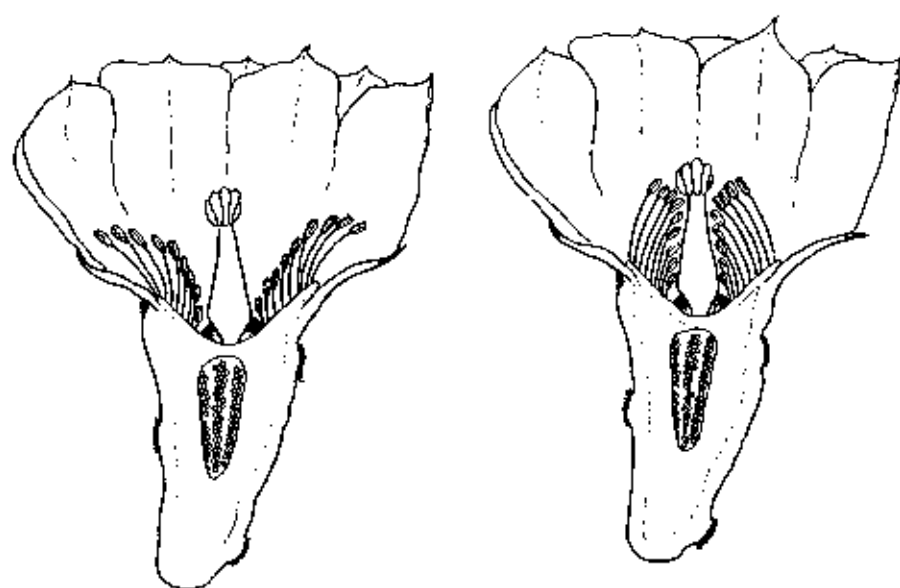


Fig. 9. Schematic section through a flower of *Opuntia brunneogemma*. Flower with non-stimulated stamens (left) and flower with stimulated stamens (right). Pollen from anthers with short filaments (lower layers) are hidden below those with long filaments (upper layer). The nectar groove is at the base of the style

Table 4. Pollen and nectar collection by females in flowers of *Opuntia brunneogemma* and *O. viridirubra* with stimulated stamens (\pm passive uptake of pollen)

| Bee species | Pollen collection | | | Nectar collection | Repeated flower visits at same flowers |
|-------------------------------|--------------------|--------------------|-----------------|-------------------|--|
| | from upper anthers | from lower anthers | pollen gleaning | | |
| <i>Ptilothrix fructifera</i> | + | + | - | + | - |
| <i>Lithurgus rufiventris</i> | + | + | - | + | - |
| <i>Cephalocolletes rugata</i> | + | + | - | + | - |
| <i>Ancyloscelis fiebrigi</i> | | \pm | | + | - |
| <i>Archysoxys cactorum</i> | - | \pm | - | + | - |
| <i>Alloscirtetica giba</i> | + | - | | - | + |
| <i>Apis mellifera</i> | + | | - | | + |
| <i>Tetrapedia rugulosa</i> | + | - | - | - | + |
| <i>Trigona spinipes</i> | + | | + | - | + |
| <i>Augochlora amphitrite</i> | + | - | + | | + |
| <i>Dialictus</i> sp. | - | ? | + | + | - |

visitors. In the lower layers we recorded about 80% of the pollen of an *Opuntia*-flower. Furthermore, the long, stimulated stamens hinder the access of visitors to the nectar groove at the bottom of the flower. The distance from the upper layer to the nectar groove in flowers with stimulated stamens is 17–25 mm in flowers of *O. brunneogemma* and 16–21 mm in those of *O. viridirubra*. Ten to 20 minutes after stimulation, the stamens bend back to their original position. During the first two to three hours of anthesis, the sensitivity of the stamens is high. As young *Opuntia* flowers are frequently visited by bees, their stamens remain in the stimulated position. This is the period in which most pollen is collected. Later during anthesis, the sensitivity of the stamens decreases.

Behaviour of the bees in flowers with stimulated stamens. The bee species can be arranged in four groups according to the females' behaviour during pollen and nectar collection in flowers with stimulated stamens (Table 4):

1. Bees collecting pollen from the lower anthers. Females of *Ptilothrix fructifera*, *Lithurgus rufiventris* and *Cephalocolletes rugata* collect the pollen which is hidden in the lower layers of anthers. To get to the lower layers, they crawl down between the innermost stamens and the style (Fig. 2). Moreover, they reach the nectar groove at the base of the style. These females, which also compete for pollen of the upper layer of anthers, actively search for and collect the *Opuntia* pollen. In young, pollen-rich flowers, their flower visits last for 1 to 4 min, while those in pollen-empty flowers last for less than 10 sec. After such a long flower visit the females have touched and stimulated all stamens.

To collect pollen, females of *Ptilothrix fructifera* brush several anthers between mid- and hind-legs and between hind legs and abdomen into the hind tibiae; thereby the abdomen shortens and extends. Females of *Lithurgus rufiventris* collect pollen with their fore legs and transfer it from mid- to hind-legs into the abdominal brush.

Females of *Cephalocolletes rugata* transport pollen in a well developed abdominal brush and in the scopa of hind femur and tibia.

2. Bees collecting pollen exclusively from the upper anthers. Females of *Alloscirtetica gilva*, *Augochlora amphitrite*, *Tetrapedia rugulosa* and *Trigona spinipes* only collect pollen from the upper layer of anthers. Typically, these females subsequently visit the same flower, but never reach the lower layers of anthers. However, in older flowers with non-stimulated stamens, these bees and also honey bee workers reach the nectar groove at the bottom of the flower.

3. Gleaners. Tiny bees of the genus *Dialictus* are able to move between the stamens and to reach the nectaries of flowers with stimulated stamens. Females were observed to collect pollen adhering to the petals and to the base of the filaments, termed 'gleaning'. Gleaning was also observed in females of *Callonychium petuniae*, *Plebeia emerina*, *P. wittmanni*, *Augochlora amphitrite* and *Trigona spinipes*.

4. Bees collecting exclusively nectar in flowers with stimulated stamens. Females of *Ancyloscelis fiebrigi*, *Arhysosage cactorum*, and *Lanthanomelissa complera* visit *Opuntia* flowers to take up nectar. Even in flowers with stimulated stamens they reach the nectaries. *Ancyloscelis* females preferably collect pollen from flowers of *Convolvulaceae*, *Arhysosage* females from *Notocactaceae* flowers and *Lanthanomelissa* females from *Iridaceae* flowers.

Discussion

Stamen movements favour the effective pollinators. The great number of bee species recorded on the *Opuntia* flowers (Table 2) indicates that there is severe competition between bees for their rich pollen and nectar resources. But females of only a few oligolectic bee species share almost all the *Opuntia* pollen among themselves, namely the effective pollinators *Ptilothrix fructifera*, *Lithurgus rufiventris* and *Cephalocolletes rugata*. These bees reach the lower layers of anthers by pushing their body downwards between style and innermost stamens. This behavioural adaptation gives a competitive advantage to these oligolectic bees and guarantees them access to the main quantity of the *Opuntia* pollen.

For the *Opuntia* species, the stamen movements and, in consequence, the compartmentation of the flower's pollen resources, have an important function in their floral biology: they hide pollen from pollen thieves and reward effective pollinators with large quantities of pollen. Furthermore, the dense packing of anthers and filaments around the style forces flower-visiting bees who are efficient pollen-collectors to contact the stigma on their way to the lower layers of anthers and to the nectary.

The clumped position of the stimulated stamens creates advantages for the effective pollinators. Maintaining the stamens in their pre-anthetic position would exclude visitors who are unlikely to act as efficient pollinators in the absence of effective pollinators. This would be of disadvantage to the flower's reproductive success. Flowers which at least temporarily offer pollen and nectar to all flower visitors maintain their general attraction. In *Cactaceae*, expanded stamens might be a primitive trait. Perhaps in the *Opuntia* flowers under study here, we see a stage of a process towards the evolution of flowers which permanently hide most of their pollen under layers of anthers.

Analysing the pollen loads of the females, we found that up to 30% of the *Opuntia* pollen grains were empty. The hypothesis that this pollen came from the upper layer of anthers was rejected in the case of *O. brunneogemma* and *O. viridirubra*. We found, that pollen from the upper and lower layers of anthers have the same relative proportion of sterile grains. Other cacti species might, however, offer higher amounts of empty pollen in the upper layer.

TROLL (1922) interpreted all stamen movements as growth movements without relation to pollination. RAUH (1979) and also TOUMÉY (1899, cited in GRANT & HURD 1979) suggested that the stamen movements in *Opuntia* flowers would influence pollen adherence to the body of any flower-visiting insect. In contrast, our results show that these movements must be interpreted as adaptations to hide pollen and to offer it only to specialised pollinators.

We found that females of *Arhysosage vactorum* are the most effective pollinators of the flowers of *Notocactus* and *Gymnocalycium* species (SCHLINDWEIN 1992, SCHLINDWEIN & WITTMANN 1995). In *Notocactus*, the stamens are also highly sensitive to mechanical stimuli (RAUH 1979). When *Arhysosage*-females collect pollen in flowers of *Notocactaceae*, they also pass through the upper layer of anthers as they do in *Opuntia*-flowers to collect nectar (Table 4). Stamen movements in *Notocactaceae* might therefore play the same role as in *Opuntia* flowers.

The *Opuntia*-bees *Ptilothrix fructifera* and *Lithurgus rufiventris*. Bees of these oligolectic species show features which we interpret as adaptations to the flowers of *Opuntia brunneogemma* and *O. viridirubra*. (1) They are specialised to collect pollen and nectar only in *Opuntia* flowers where they reach the lower layers of anthers. (2) In their scopae with long, unbranched bristles, they can transport the very large *Opuntia* pollen. (3) Their flight period coincides with the flowering period of *Opuntia*. (4) Females are so abundant and predictable at *Opuntia* flowers that males patrol the flowers in search for mates.

In North America, two species of the genus *Lithurgus* are oligolectic in *Opuntia* flowers: *Lithurgus apicalis* in *O. echinocarpa* (GRANT & HURD 1979), *O. imbricata* (McFARLAND & al. 1989), *O. littoralis* (GRANT & GRANT 1979a), *O. phaeucantha* and *O. polyacantha* (OSBORN & al. 1988) and *Lithurgus gibbosus* in *O. compressa* (GRANT & al. 1979) and *O. discata* (COCKERELL 1900, cited in GRANT & al. 1979). Both *Lithurgus* species are considered to be effective pollinators of the *Opuntia* flowers they visit. In the Andes near Salta (Argentina), we recorded females of an undescribed *Lithurgus* species in the flowers of various *Opuntia* species. At the same time, males of *Ptilothrix* cf. *nigerrima* were patrolling these flowers. Thus, in geographically distant regions, various *Lithurgus* and perhaps also *Ptilothrix* species show distinct preferences to collect pollen in *Opuntia* flowers.

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