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Pollination of *Opuntia lindheimeri* and Related Species[1]

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Abstract: The large, yellow, bowl-shaped flowers of *Opuntia lindheimeri*, *O. discata*, *O. phaeacantha major*, and *O. compressa* in Texas are visited by various species of beetles and bees. The beetles and small bees (*Perdita*, *Dialictus*) are pollen thieves. The pollinators are the medium-sized and larger bees (*Melissodes*, *Diadasia*, *Lithurge*, *Megachile*, *Agapostemon*, etc.). Different species of the *Opuntia lindheimeri* group have the same pollination system and there is no evidence of any floral isolation between them. The pollination system of these species of *Opuntia* in Texas is essentially the same as that of *Echinocereus fasciculatus* and *Ferocactus wislizeni* in Arizona.

The previous paper in this series dealt with the pollination system of two species of cactus with large cup-shaped flowers in Arizona (GRANT & GRANT 1979). In the present paper we consider the cup-shaped flowers of four species of *Opuntia* in Texas and their pollinators. It will be shown that the pollination system of the *Opuntia lindheimeri* group in central Texas is the same in its general features as that of *Echinocereus fasciculatus* and *Ferocactus wislizeni* in Arizona.

While a number of insects, principally those of the *Holometabola* (especially *Coleoptera*, *Lepidoptera*, *Diptera* and *Hymenoptera*) are known to visit flowers of *Opuntia*, only certain groups of *Coleoptera* e.g., *Melyridae*, *Nitidulidae* and *Scarabaeidae*) and *Hymenoptera* (particularly native bees) are involved in the pollination of these flowers. All evidence accumulated to date suggests that while certain species of *Coleoptera* are involved in the intrafloral ecology of *Opuntia*, their role in the pollination of these plants is only incidental to their intrafloral activities. However, even though the intrafloral relationships of *Opuntia*-visiting bees, as a group, are varied and range in pollination

[1] Pollination of North American Cacti, II.—See GRANT & GRANT (1979).

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capabilities from scarcely, if any, to virtually obligate pollinators, this group is unquestionably the most important assemblage involved in the pollination of these plants.

Nearly 100 species of native bees in America north of Mexico are known to visit the flowers of *Opuntia* (HURD 1978; GRANT & HURD, in press). Although there is some information available in the literature which indicates that at least some of the pollen-collecting species visit these flowers for nectar, pollen or both, the majority of the published records not only lack these data, but are also without supporting observations on the intrafloral behavior of these visitors. Additionally, only infrequently are the species level taxa of *Opuntia* specified in the published reports.

Species and Populations Studied

The species considered in this study are *Opuntia lindheimeri* ENGELM., *O. discata* GRIFFITHS, *O. phaeacantha* var. *major* ENGELM., and *O. compressa* (SALISB.) MACBR. These species are closely related and hybridize in nature. BENSON (1969 a) places them together in the taxonomic series *Opuntiae*, distinguished by reddish fleshy fruits with small seeds. Further taxonomic details on the species are given by BENSON (1969 a, 1969 b). We follow BENSON (1969 b) on taxonomy except that we are recognizing *O. discata* as a taxonomic species rather than as a variety of *O. phaeacantha* for reasons which will be given elsewhere.

The four species under consideration are all widespread in Texas. All extend to other areas. *Opuntia lindheimeri* extends beyond Texas to Louisiana and Mexico, *O. compressa* to the Midwest and eastern United States, *O. phaeacantha* var. *major* to the Great Plains and desert Southwest, and *O. discata* to the desert Southwest and Mexico. Our observations of them reported here are confined to an area in central and south-central Texas.

The populations studied and their localities are as follows. *Opuntia lindheimeri*: (1) Kyle, Hays County; (2) Brackenridge Field Area, Austin, Travis Co.; (3) northwest of Austin, Travis Co.; (4) Lake Amistad, west of Del Rio, Val Verde Co. *Opuntia discata*: (5) Pedernales Falls, Pedernales State Park, Blanco Co.; (6) Lake Amistad, west of Del Rio, Val Verde Co. *Opuntia phaeacantha* var *major*: (7) Wolf Mt. trail, Pedernales State Park, Blanco Co. *Opuntia compressa*: (8) Brackenridge Field Area, Austin, Travis Co. The studies were made in April and May of 1977 and 1978.

Floral Mechanism of *Opuntia lindheimeri*

The perianth is large, deep lemon-yellow, and bowl-shaped, and the flowers have a slight sweet fragrance. The outside diameter of the perianth ranges from 5 to 10 cm, depending on whether the perianth parts are arched up to form a narrow bowl, or are spread out to form a broad bowl. The perianth is about 5 cm high from base to top. No nectar could be detected.

The numerous yellowish stamens surround the massive central style. The green stigma is composed of about 8 erect lobes contracted into a knob-like structure. The stigma stands well above the anthers in the center of the flower and affords a landing platform for some kinds of bees.

The stamens are sensitive to contact. When touched, the filaments bend in the direction of the contact. They bend inwards towards the style if touched on the inner side, and outwards towards the perianth if touched on the outer side.

Each flower remains open for one day. Early in the day the anthers dehisce and expose the yellow pollen. We do not know yet just when in the day the stigma becomes receptive (this question is being investigated), but clearly there is some overlap in time between the male and female phases.

There is a continuous succession of flowers on the plants during the blooming season. This season is relatively short. It lasts from early May to late May in the Austin area in central Texas, and, as would be expected, comes earlier, in April, in south Texas.

When a flower is through blooming, the perianth and androecium wither and drop off the inferior ovary. A well-defined abscission layer develops between the top of the ovary and the perianth, permitting a clean separation of these two floral organs.

The statement made earlier that the stigma is elevated well above the anthers is true of flowers in the height of the blooming season. Some flowers observed at the end of the blooming season do not have elevated stigmas, but instead have anthers and stigma on the same level. The early and mid-season flowers are non-autogamous and do not set seeds without insect vectors, as indicated by experimental tests. The late-season flowers, or at least some of them, are apparently autogamous. This latter situation requires further study to determine whether it is a regular or an aberrant phenomenon.

Floral Mechanism of *Opuntia discata*, *O. phaeacantha* var. *major* and *O. compressa*

The floral mechanism in the central Texas populations of these species is generally similar to that of *O. lindheimeri*. It is unnecessary to repeat the details. The perianth is slightly smaller in *O. discata*, *O. phaeacantha* var. *major*, and *O. compressa* than it is in *O. lindheimeri*. Perianth color in these species may be all yellow, as in *O. lindheimeri*, but may also be yellow with a red center.

The three taxa under consideration here all exhibit sensitive stamens as does *O. lindheimeri*. All species have stigmas elevated above

the anthers in flowers in the early and middle part of the blooming season. At least some flowers of *O. discata* and *O. phaeacantha* var. *major* at the end of the blooming season have stigmas on the same level as the anthers, as noted also in *O. lindheimeri*.

Breeding System

Next to nothing is known about breeding systems in *Opuntia* or indeed in the *Cactaceae*. We have begun to study this subject in the *Opuntia lindheimeri* group. Selected individuals of the Kyle and Brackenridge populations of *O. lindheimeri* have been subjected to routine tests for self-compatibility and autogamy in our experimental garden in Austin.

Flowers of *O. lindheimeri* from Kyle and Brackenridge which were artificially self-pollinated and bagged, produced normal fruits filled with seeds, whereas bagged flowers alone did not produce fruits. The plants are thus self-compatible but non-autogamous. Further work along these lines is needed and is currently underway.

Beetle Visitors

Two classes of insect visitors were common in the flowers of all populations of the *Opuntia lindheimeri* group in central Texas, bees and beetles. The behavior and role of these two groups of insects are quite different.

The following species of beetles were found in flowers in at least one *Opuntia* population and usually in two or more populations. (1) *Euphoria kerni* HALDEMAN (*Scarabaeidae*); (2) *Diabrotica undecimpunctata howardi* BARBER (*Chrysomelidae*); (3) *Nodonta puncticollis* (SAY) (*Chrysomelidae*); (4-5) *Acmaeodera neglecta* FALL and *A. ornatoides* BARR (*Buprestidae*); (6) *Carpophilus floralis* ER. (*Nitidulidae*); (7) *Hypebaeus* sp. (*Melyridae*); (8) *Trichochrous* sp. (*Melyridae*); and (9) *Tanaops* sp. (*Melyridae*).

The moderately large scarab, *Euphoria kerni*, and the small nitidulid, *Carpophilus floralis*, were virtually ubiquitous in flowers of different populations. The *Carpophilus* beetles, furthermore, were not only widespread but also abundant, often being represented by scores or even hundreds of individuals in a single flower.

The beetles camp in the base of the flowers, feedings on the stamens and sometimes on the petals. Some pollen adheres to their body hairs. The beetles do not fly from flower to flower very often. When they do approach a new flower they are likely to land on the perianth or stamens, bypassing the stigma. In view of their sedentary habits, their

usually scanty pollen loads, and their tendency to bypass the stigma, one would have to conclude that the beetles are relatively ineffective as pollinators. Probably some of the beetles, especially the common *Carpophilus* and *Euphoria* beetles, do carry out some pollination, but not very much.

On the other hand, the beetles are highly destructive in some flowers. We have found flowers of *Opuntia lindheimeri* inhabited by numerous *Carpophilus* beetles and one or two *Euphoria* beetles in which the stamens had been devoured completely, leaving only a bare perianth cup and the intact central style. However, the beetles are unable to get to the ovules in the inferior ovary. The inferior position of the ovary is probably a first line of defense against beetles, and the decidous habit of the perianth and androecium, mentioned earlier, may well be an additional means of protection of the ovules. Flowers whose stamens are devoured by the beetles go on to set good fruits.

Bee Visitors

We have found ten species of bees on flowers of the *Opuntia lindheimeri* group in central Texas. These are listed in Table 1. Other investigators have recorded some of these and a few additional bees (some not identified as to species) on *O. lindheimeri* and its relatives, mostly in Texas but also in New Mexico, and these are listed in Table 2.

Four of the species are oligoleges of the *Cactaceae*: *Perdita texana (Andrenidae)*, *Lithurge gibbosus* and *L. sp. (Megachilidae)*, and *Diadasia rinconis (Anthophoridae)*. *Perdita texana* is interesting in that it collects pollen only from *Opuntia* flowers so far as is known (BARROWS & al. 1976). It does not necessarily follow, of course, that *Opuntia* gains anything from the visits of *Perdita texana*. The remaining species on the list in Table 2 are polyleges and obtain their nectar and pollen from a wide variety of sources in addition to the *Cactaceae*.

The female bees of the various species forage in the stamen mass, collect pollen for their nests, and unintentionally pick up more pollen on their bodies mechanically. The members of some bee species, however, do not ordinarily come into contact with the stigma, and therefore are not regular pollinators.

Body size and intrafloral behavior of bees are important factors in pollination effectiveness in *Opuntia* flowers. The very small bees, *Perdita texana* and *Dialictus papillosus*, can and do slip into a flower without contacting the stigma. Furthermore, as noted by BARROWS & al. (1976), a small bee like *Perdita texana* will obtain a full pollen load from one flower, and does not often fly from flower to flower. For these reasons the very small bees are apparently not effective pollinators of the *Opuntia lindheimeri* group.

Table 1. Bee species collected by us in flowers of the *Opuntia lindheimeri* group in central Texas.

Bee species	*Opuntia* species and population*
Diadasia rinconis COCKERELL (*Anthophoridae: Anthophorinae*)	*lind* Kyle, *lind* Brackenridge, *disc* Pedernales
Melissodes tristis COCKERELL (*Anthophoridae: Anthophorinae*)	*lind* Brackenridge
Ceratina dupla SAY (*Anthophoridae: Xylocopinae*)	*lind* Brackenridge
Xylocopa virginica texana CRESSON (seen, not collected) (*Anthophoridae: Xylocopinae*)	*lind* Kyle
Apis mellifera LINN (*Apidae*)	*lind* Kyle
Lithurge gibbosus (SMITH) (*Megachilidae*)	*comp* Brackenridge
Megachile amica CRESSON (*Megachilidae*)	*phaea* Pedernales
Agapostemon texanus CRESSON (*Halictidae*)	*lind* Brackenridge, *comp* Brackenridge, *disc* Pedernales, *phaea* Pedernales
Dialictus pilosus (SMITH) (*Halictidae*)	*lind* Brackenridge, *comp* Brackenridge, *disc* Pedernales
Perdita texana (CRESSON) (*Andrenidae*)	*lind* NW Austin, *lind* Amistad, *disc* Amistad, *disc* Pedernales

* Self-evident abbreviations are given here; refer to the section on materials and study areas for details.

Bee Pollinators

The key to bee pollination in these *Opuntia* flowers lies in the bees' intrafloral behavior which culminates in stigmatic contact. The conformation of the flowers, with a bowl-shaped perianth and a central stigma, is such as to route the medium-sized and larger bees by the stigma in their visitations. As a matter of observation, the medium-sized and larger bees normally land on the stigma in their approach to a new flower, and then crawl down into the stamen mass. Yellow *Opuntia* pollen can be found on the stigmas after such visits. Furthermore, the larger bees fly frequently from flower to flower to collect their pollen loads, and this enhances their value as pollinators (BARROWS & al. 1976).

Pooling the valuable observations of BARROWS & al. (1976) with our own, the main pollinators of the *Opuntia lindheimeri* group would be the medium-sized and larger bees of the genera *Diadasia, Melissodes,*

Table 2. Summary of records of bee species on flowers of the *Opuntia lindheimeri* group. Collection sites in Texas in nearly all cases.

Opuntia species	Bee species	Authority
O. lindheimeri	*Melissodes tepaneca* CRESSON	LABERGE 1956 a
	Melissodes opuntiella COCKERELL	LABERGE 1956 b
	Melissodes coreopsis ROBERTSON	LABERGE 1961
	Melissodes tristis COCKERELL	LABERGE 1961; and this paper
	Diadasia rinconis COCKERELL	new record
	Ceratina dupla SAY	new record
	Xylocopa virginica texana CRESSON	new record
	Apis mellifera LINN.	new record
	Agapostemon texanus CRESSON	new record
	Dialictus pilosus (SMITH)	new record
	Perdita texana (CRESSON)	new record
O. phaeacantha var. *major*	*Melissodes* sp.	BARROWS & al. 1976
	Xylocopa sp.	BARROWS & al. 1976
	Bombus sp.	BARROWS & al. 1976
	Megachile sp.	BARROWS & al. 1976
	Megachile amica CRESSON	new record
	Lithurge sp.	BARROWS & al. 1976
	Agapostemon texanus CRESSON	new record
	Perdita texana (CRESSON)	BARROWS & al. 1976
O. discata	*Lithurge gibbosus* (SMITH)	COCKERELL 1900[1,2]
	Diadasia rinconis COCKERELL	new record
	Agapostemon texanus CRESSON	new record
	Dialictus pilosus (SMITH)	new record
	Perdita texana (CRESSON)	new record
O. macrorhiza	*Melissodes coreopsis* ROBERTSON	LABERGE 1961
	Melissodes tristis COCKERELL	LABERGE 1961
	Ceratina shinnersi DALY	DALY 1973
O. compressa	*Lithurge gibbosus* (SMITH)	new record
	Megachile addenda CRESSON	MITCHELL 1935[3]
	Agapostemon texanus CRESSON	new record
	Dialictus pilosus (SMITH)	new record

[1] Las Cruces, New Mexico
[2] Reported under old name *Opuntia engelmannii*
[3] Reported under old name *Opuntia vulgaris*

Xylocopa, *Bombus*, *Apis*, *Lithurge*, *Megachile*, and *Agapostemon*. In the populations we studied, *Agapostemon* was more common and was bringing about more pollination than the other genera of bees.

One finds the same bee species on different *Opuntia* species in the

same area (Table 1). The floral mechanisms of the species of the *Opuntia lindheimeri* group considered here present no known barrier to interspecific pollination.

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