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Pollination of the Southwestern Opuntias[1]

By

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Abstract: This paper presents an overview of pollination systems in *Opuntia* sens. lat. in the southwestern United States. The floral syndrome of large, colorful, bowl-shaped, diurnal flowers is present in all of the prickly-pear species and most of the cholla (*Cylindropuntia*) species in this area. Pollination by medium-sized and large bees is established for some of the species with this floral syndrome and is predicted for the others. The same floral syndrome is widespread in *Opuntia* in other geographical areas.—Deviations from this floral syndrome occur in certain species of southwestern chollas, one of which has nocturnal disc-shaped flowers, and in several tropical American species groups or segregate genera with red hummingbird flowers. But such cases are relatively infrequent. Divergence between species with respect to floral syndrome and pollination system is not a common feature in the evolutionary pattern of *Opuntia*.

In this paper we will attempt to give an overview of the genus *Opuntia* in the American Southwest with respect to pollination systems. It is now possible to make some reliable generalizations about the pollination systems in the *Opuntia* flora of this region. We can also see more clearly now some problem areas which are worthy of future investigation, and we call attention to these.

General Features of the Southwestern *Opuntia* Flora

The American Southwest, defined for our present purpose as the region from southern California to Texas, is an important center of distribution of the genus *Opuntia*. There are about 38 native taxonomic

[1] Pollination of North American Cacti, IV.—Previons parts of this series: Grant & Grant 1979 a, Grant & al. 1979, Grant & Grant 1979 b.

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species in this area, depending on the treatment of some species of uncertain status, and in addition one widespread naturalized species, *O. ficus-indica* (L.) MILL. The southwestern *Opuntia* flora is not only relatively rich in species, but is also well known taxonomically, thanks to the critical studies of BENSON (1969a, 1969b, 1969c). We also have an empirical data base now on the pollination ecology of southwestern cacti which will support extrapolations and generalizations pertaining to the *Opuntia* flora of this area (GRANT & GRANT 1979a, 1979b, GRANT & al. 1979).

A generalized treatment of the pollination ecology of *Opuntia* would not be very fruitful or even feasible at present for other geographical regions inhabited by this large and widespread genus for the following reasons. The *Opuntia* flora drops off rapidly in species diversity in areas to the north and east of the American Southwest. The genus has other rich centers of distribution to the south—in Mexico, Brazil, the Andes, etc.—but here the plants are poorly known taxonomically and scarcely anything is known about their intrafloral ecology.

The Opuntias of the Southwest fall into three distinct groups: *Cylindropuntia*, *Corynopuntia*, and *Opuntia* s. str. (or *Platyopuntia*). Some students (BRITTON & ROSE 1963; BENSON 1969a, 1969b) treat these groups as subgenera and sections of a large collective genus *Opuntia*. Others (BACKEBERG 1970; EARLE 1963) recognize them as segregate genera. We happen to prefer the three-genus system of classification for these plants, because it reflects the distinctness of the three lines, but we will follow the more conservative single-genus treatment for the purpose of this study.

The prickly-pears (*Opuntia* s. str.) and cholla cacti (*Cylindropuntia*) are about equal in species diversity, with 17 native taxonomic species each in the southwestern area; but the prickly-pears are more common and more widespread. The club-chollas (*Corynopuntia*) form a smaller group, with four species in our area, and these are relatively uncommon.

The greatest morphological diversity in the southwestern Opuntias is in vegetative characters, and indeed, it is on vegetative characters that the Opuntias are subdivided into the three main groups mentioned above.

The southwestern Opuntias also exhibit morphological variation in their fruits. Fleshy fruits and dry fruits characterize different series within each of the two larger groups, the cholla cacti and the prickly-pears.

On the other hand, floral characters are relatively uniform among the southwestern species of *Opuntia* s. lat. An indication of this is the fact that floral characters are not diagnostic of subgenera, sections, or

series; and are used only occasionally to separate related species belonging to the same section or series. The relative uniformity in floral characters is particularly true of the prickly-pear Opuntias. Some interesting deviations from the general type are found in the cholla cacti.

Flowers of Prickly-Pear Opuntias

The basic floral syndrome in the southwestern prickly-pears consists of the following features: solitary, large size, bowl or cup shape, many perianth segments, brightly colored perianth, diurnal periodicity, many yellow stamens, and massive central style and stigma. (Some other features will be mentioned later.) This syndrome is found in all 17 species.

Flower diameter is a measure of flower size which can be taken from the species descriptions given by BENSON (1969 a, 1969 b, 1969 c). The normal maximum flower diameters in each of the 17 species form a continuous and even distribution from 5 cm to 9 cm with no single peak.

The most common and widespread flower color in the group is yellow. The flowers may be either uniformly yellow or yellow with a red center. Magenta or pink flowers are less common, occurring in four species. Three of these species (*O. basilaris*, *O. nicholii* L. BENSON, and *O. erinacea* ENGELM. & BIGELOW) are characteristically magenta or pink-flowered, but also have yellow-flowered races. A fourth species (*O. littoralis*) is usually yellow-flowered, but has a reddish-flowered race.

The stamens are thigmotropically sensitive, the filaments bending and moving in response to contact. This is a widespread characteristic, not only in the southwestern prickly-pears, but in *Opuntia* s. str. as a whole (TOUMEY 1899; KNUTH 1906—1909; PORSCH 1938). Whether there are any exceptional species without sensitive stamens remains to be determined. It is usually stated that the stamens bend inward towards the style when triggered off (TOUMEY 1899), and we can confirm that this is often the case. However, we have also observed cases in *O. lindheimeri* and *O. discata* in which the stamens bend towards the point of contact whether this is inward or outward (GRANT & al. 1979). How common this latter type of stamen movement is is not known.

The function of stamen sensitivity in *Opuntia* has not been satisfactorily explained. TOUMEY (1899) made the interesting suggestion that the stamen movements facilitate the depositing of pollen on the insects' bodies. But the insects can and do pick up pollen as a result of their foraging behavior or breeding habits without stamen movements. Furthermore, as will be noted later, the critical link in the pollination process is not pollen pickup but stigmatic contact. An alternative

suggestion is that the stamen movements stimulate an insect to leave a flower by going up the style and over the stigma (PORSCH 1938). But this would only promote self-pollination. Also, insects do not usually follow this route out of *Opuntia* flowers according to our observations.

The central stigma forms a good landing platform and perching place for some insects. The stigma is usually but not invariably elevated above the stamens. It goes without saying that pollination depends on an insects' contacting both the anthers and the stigma while transporting viable pollen. Most insect visitors do become covered with pollen, but not all of these come into contact with the stigma.

The flowers of some species of prickly-pear Opuntias have no detectable nectar. Other species do furnish nectar; a detailed study of the basal nectary in one such species is given by DAUMANN (1930). The systematic and geographical distribution of nectariferous flowers within the prickly-pear subgenus or segregate genus is unknown. A possibility to investigate is that loss of nectar production in prickly-pear Opuntias is correlated with aridity and the need for moisture conservation.

Beetle Visitors

Prickly-pear flowers are commonly inhabited by the small nitidulid beetle *Carpophilus*. We have records from numerous *Opuntia* populations from southern California to Texas. The species of *Carpophilus* involved are *C. pallipennis* (SAY) in California and Arizona and *C. floralis* ERICHSON in Texas. *Carpophilus* is by no means restricted to cactus flowers, for we have found it in flowers of Yucca, *Calochortus* and so forth, but in our experience it occurs more frequently in the flowers of cacti than in those of other plant groups.

The frequent occurrence of *Carpophilus pallipennis* in *Opuntia* flowers was noted long ago by TOUMEY (1899), PARSONS (1943), and more recently by BENSON and WALKINGTON (1965). PARSONS (1943) in his monograph of *Nitidulidae* states for *C. pallipennis*: "This species is abundant on the flowers of prickly pear..."; und he makes a similar comment about *C. floralis*. The *Carpophilus* beetles camp in the base of the flowers where they chew on the stamens and sometimes on the petals. Large numbers of them often accumulate in a single flower. Pollen grains frequently adhere to their body hairs.

The nature of the association between *Carpophilus* beetles and cactus flowers—whether it is a mutually beneficial one or a unilateral benefit to the beetles—is not clear. In our earlier field studies of cactus flowers we were inclined to believe that the *Carpophilus* beetles are significant pollinating agents. We were assuming then that the beetles would regularly contact the stigma. However, we have not actually

observed them on the stigma, and limited observations suggest that they do not use the stigma as a landing platform. They are usually in the stamen mass, as already noted, and do not often fly from flower to flower; and when they do fly into a new flower they are likely to bypass the stigma. For these reasons we now believe that *Carpophilus* is only an occasional pollinator of cacti. Further study is needed.

Trichochrous spp. (*Melyridae*) form another group of common and widespread visitors to prickly-pear and other cactus flowers. We have recorded *Trichochrous* in flowers of *Opuntia chlorotica* ENGELM. & BIGELOW (Calif.), *O. basilaris* ENGELM. & BIGELOW (Calif.), *O. lindheimeri* ENGELM. (Texas), *O. edwardsii* V. & K. GRANT (Texas), and *Echinocereus fasciculatus* (ENGELM.) BENSON (Arizona). *Trichochrous* shows less preference for cactus flowers than does *Carpophilus*, being found commonly in flowers of many other plant families. Otherwise the remarks made above concerning *Carpophilus* are applicable also to *Trichochrous*. This small flower beetle gets into the stamen mass, picks up pollen on its body hairs, and could be a pollen vector. However, it probably does not contact the stigma often while mechanically transporting viable pollen, and it is probably not a significant pollinating agent in southwestern Opuntias to judge from our observations.

Among other genera and families of beetles found in southwestern prickly pear flowers are *Nodonta (Chrysomelidae)*, *Acmaeodera (Buprestidae)*, and *Euphoria (Scarabaeidae)*. The moderately large scarab, *Euphoria kerni* HALDEMAN, is often represented by a single individual per flower in Texas populations of prickly-pear Opuntias. It seems to be mainly destructive of these flowers, because of its observed feeding habits (GRANT & al. 1979).

In our early work on southwestern Opuntias years ago we categorized the pollination system as bee-and-beetle pollination. BENSON & WALKINGTON (1965) have expressed the same view. With the accumulation of more evidence in subsequent field studies it has become apparent that the beetles, while common flower visitors, are not regular pollinators.

Bee Visitors

Two previous papers in this series (GRANT & al. 1979; GRANT & GRANT 1979 b) give lists of bee species for several species of southwestern prickly-pear Opuntias. It is established by these studies that the medium-sized and larger bees are the important regular pollinators of these Opuntias.

The wide range of bee visitors to *Opuntia* flowers is shown by the species list in Table 1. This list is made from a computer printout of

Table 1. Bee species recorded on flowers of *Opuntia* in the United States. Compiled from computer printout of records in HURD (1978 b).

Family and Genus	Species
Colletidae	
Colletes	*C. brevicornis* ROBERTSON.
Hylaeus	*H. polifolii* (COCKERELL).
Andrenidae	
Andrena	*A. fracta* CASAD and COCKERELL. *A. hallii* DUNNING. *A. prunorum* COCKERELL.
Megandrena	*M. enceliae* (COCKERELL).
Perdita	*P. bidenticauda* TIMBERLAKE. *P. californica* (CRESSON). *P. claypolei* TIMBERLAKE. *P. crassa* TIMBERLAKE. *P. eysenhardtiae* TIMBERLAKE. *P. lobata* TIMBERLAKE. *P. opuntiae* COCKERELL. *P. polytropica* TIMBERLAKE. *P. robertsi* TIMBERLAKE. *P. texana* (CRESSON).
Halictidae	
Augochlorella	*A. aurata* (SMITH). *A. gratiosa* (SMITH). *A. neglectula* (COCKERELL). *A. pomoniella* (COCKERELL). *A. striata* (PROVANCHER).
Dialictus	*D. coreopsis* (ROBERTSON). *D. nymphalis* (SMITH). *D. pilosus* (SMITH).
Megachilidae	
Asheadiella	*A. cactorum* (COCKERELL). *A. meliloti* (COCKERELL). *A. opuntiae* (COCKERELL).
Chalicodoma	*C. browni* (MITCHELL). *C. subexilis* (COCKERELL).
Heriades	*H. gracilior* COCKERELL. *H. occidentalis* MICHENER.
Hoplitis	*H. albifrons* (CRESSON).
Lithurge	*L. apicalis* (CRESSON). *L. gibbosus* (SMITH).
Megachile	*M. addenda* CRESSON. *M. amica* CRESSON. *M. anograe* COCKERELL. *M. brevis* MITCHELL. *M. casadae* COCKERELL. *M. frugalis* CRESSON. *M. gentilis* CRESSON. *M. lippiae* COCKERELL. *M. mendica* CRESSON. *M. montivaga* CRESSON. *M. newberryae* COCKERELL. *M. policaris* SAY. *M. sidalceae* COCKERELL. *M. texana* CRESSON.
Anthophoridae	
Anthophora	*A. fedorica* COCKERNELL.
Ceratina	*C. acantha* PROVANCHER. *C. apacheorum* DALY. *C. dupla* SAY. *C. nanula* COCKERELL. *C. neomexicana* COCKERELL. *C. pacifica* SMITH. *C. shinnersi* DALY. *C. texana* DALY.
Diadasia	*D. australis* (CRESSON). *D. opuntiae* COCKERELL. *D. piercei* COCKERELL. *D. rinconis* COCKERELL.
Exomalopsis	*E. nitens* COCKERELL. *E. torticornis* COCKERELL.
Melissodes	*M. blanda* LABERGE. *M. communis* COCKERELL. *M. coreopsis* ROBERTSON. *M. mitchelli* LABERGE. *M. opuntiella* COCKERELL. *M. paroselae* COCKERELL. *M. paucipuncta* LABERGE. *M. tepaneca* CRESSON. *M. tessellata* LABERGE. *M. tristis* COCKERELL. *M. wheeleri* COCKERELL.
Svastra	*S. petulca* (CRESSON).
Xylocopa	*X. virginica* LINN.

records of bee species visiting *Opuntia* in HURD (1978 b). The list does not include the *Apidae*. The records are for bees in temperate North America, and for visits to flowers of unidentified species of *Opuntia*. However, since the Southwest is the center of distribution of *Opuntia* in temperate North America, and since prickly-pear Opuntias are the most prevalent subgroup, the list is certain to be weighted heavily in favor of visits to southwestern prickly-pears. Table 1 lists 76 species of bees known to visit *Opuntia* flowers.

This list can be extended by records from other sources: from our studies cited above; from reports of MICHENER (1937, 1938, 1939, 1954), and from unpublished records in the collection of P. H. TIMBERLAKE. These additional species are grouped by family and listed below. The megachilids are recorded by MICHENER, the other bees by TIMBERLAKE and ourselves. These additional records bring the total number of bee species known to visit *Opuntia* flowers in North America to 90.

Halictidae: Agapostemon angelicus COCKERELL; *A. femoratus* CRAWFORD; *A. texanus* CRESSON; *Dialictus incompletus* (CRAWFORD); *D. tegulariformis* (CRAWFORD); *Evylaeus cooleyi* (CRAWFORD); *Halictus tripartitus* COCKERELL. *Megachilidae: Ashmeadiella maxima* MICHENER; *A. stevensi* MICHENER. *Heriades timberlakei* MICHENER; *Lithurge bruesi* MITCHELL. *Anthophoridae: Anthophora fulvicauda* TIMBERLAKE. *Apidae: Apis mellifera* LINN.; *Bombus californicus* SMITH.

While no species of bees belonging to the families *Melittidae* and *Oxaeidae* are known to visit the flowers of *Opuntia*, many pollen-collecting species of the other six families of bees present in America north of Mexico have been recorded from these flowers. Their numbers are: *Colletidae* (2 species), *Andrenidae* (14 species), *Halictidae* (15 species), *Megachilidae* (28 species), *Anthophoridae* (29 species), and *Apidae* (2 species, including the introduced European honeybee, *Apis mellifera* LINN.).

Most bee species recorded on *Opuntia* are polylectic, collecting pollen from a wide range of plant groups. Only certain pollen-collecting species of relatively few genera in the families *Andrenidae, Megachilidae,* and *Anthophoridae* have evolved as oligoleges of *Opuntia*. These genera containing *Opuntia* oligoleges are *Perdita, Lithurge, Ashmeadiella, Diadasia,* and *Melissodes*. (For reviews of floral constancy and oligolecty, see GRANT 1950; LINSLEY 1958; and BAKER & HURD 1968.)

At present, there are no species of pollen-collecting bees known to have evolved an intrafloral relationship solely with a single taxon of *Opuntia*. One conceivable exception is if a specific (or infraspecific) taxon is the sole member of *Opuntia* in a local or even regional flora which is being visited by an oligolege of wider geographic occurrence

which thereby also visits other specific (or infraspecific) taxa of *Opuntia*. Even so this localized or even regionalized situation can hardly be interpreted as a major coevolutionary relationship, although theoretically it may serve as an initial basis for coevolution in one or more geographically differentiating biotas.

The fact that a bee species is oligolectic on *Opuntia* does not mean that it is a specific pollinator of *Opuntia*. *Perdita texana* is an interesting example of this. So far as known it collects pollen only from *Opuntia* (BARROWS & al. 1976), but it is not an important or regular pollinator of *Opuntia* (BARROWS & al. 1976; GRANT & al. 1979). *Perdita texana* is a small bee which ordinarily slips into and out of an *Opuntia* flower without contacting the stigma.

All bee visitors can be presumed to pick up pollen. However, a critical step in pollination of prickly-pear Opuntias is the transfer of viable pollen to a receptive stigma. The medium-sized and larger bees, but usually not the smaller bees or beetles, generally alight on the stigma in their initial approach to a flower, thereby enhancing the likelihood of pollination.

A few cleptoparasitic species of bees (e.g., *Sphecodes* spp., *Triepeolus* spp.) are known to visit the flowers of *Opuntia*, but their role in the pollination of these flowers must be viewed as accidental and fortuitous since they seek nectar, sometimes in company with their pollen-collecting hosts, and only rarely transport pollen (mechanically) incidental to such visits. Males of some *Opuntia* oligoleges (e.g., *Diadasia* spp.) doubtless are important in the transfer of pollen not only because of the regularity of their visits to these flowers for mating activities and energy, but also because pollen readily adheres to the body hairs of these medium-sized bees and does come in contact with receptive stigmas as they fly from flower to flower (in search of females and food), often utilizing the stigma as the focus of their landing operation.

Cholla Cacti

The southwestern species of *Opuntia* subgenus *Cylindropuntia* are more variable in their flower characters than are the prickly-pear Opuntias. Three groups are recognized here.

One group containing 10 species [including *O. imbricata* (HAW.) DC., *O. spinosior* (ENGELM.) TOUMEY, *O. versicolor* ENGELM., and others] has large cup-shaped flowers with flower diameters ranging from 4 to 8 cm. Such flowers are similar to those of prickly-pears in size and form. In color, they may be yellow, like most prickly-pears, but more often are purple, greenish, or some other color.

Table 2. Records of bee species on flowers of southwestern cholla cacti.

Opuntia species	Bee species	Authority
O. imbricata (HAW.) DC. (Reported under *O. arborescens* ENGELM.)	*Lithurge apicalis* CRESSON (*Megachilidae*)	(COCKERELL 1900)
O. echinocarpa ENGELM. & BIGELOW	*Andrena enceliae* (COCKERELL) (*Andrenidae*)	(HURD 1978b)
	Lithurge apicalis (CRESSON) (*Megachilidae*)	(HURD 1978b)
	Ashmeadiella opuntiae (COCKERELL) (*Megachilidae*)	(HURD 1978b)
O. parryi ENGELM.	*Agapostemon angelicus* COCKERELL (*Halictidae*)	(TIMBERLAKE, unpubl.)
	Agapostemon texanus californicus COCKERELL	(TIMBERLAKE, unpubl.)
	Dialictus incompletus (CRAWFORD) (*Halictidae*)	(TIMBERLAKE, unpubl.)
	Ashmeadiella opuntiae (COCKERELL) (*Megachilidae*)	(HURD 1978b)
	Exomalopsis nitens COCKERELL (*Anthophoridae*)	(HURD 1978b)
	Melissodes tessellata LABERGE (*Anthophoridae*)	(HURD 1978b)

Detailed studies have not been made of pollination in this group of large-flowered cholla cacti. There is every reason to believe that they have the same pollination system as the southwestern prickly-pears with similar flower characters. Some fragmentary records of bee visitors to three species in this group of chollas are given in Table 2.

Another group of southwestern cholla species is characterized by small flowers about 1 cm in diameter. *Opuntia ramosissima* ENGELM. and *O. leptocaulis* DC. belong in this group. Nothing is known about the pollination of these small-flowered chollas. Field observations are much needed.

A third group of species bear medium-sized flowers but produce fruits with few sound seeds and rely chiefly on vegetative propagation for reproduction. *Opuntia bigelovii* ENGELM. and *O. fulgida* ENGELM. of Arizona and bordering areas are examples. Both species reproduce freely from the deciduous stem-joints, whereas seedlings are rare or unknown.

Opuntia bigelovii has cup-shaped, greenish-yellow flowers, which are

apparently fertile, but these produce mostly sterile fruits. TOUMEY (1895) examined 50 fruits; 48 of these contained no seeds; and two fruits each contained one seed.

Opuntia fulgida is a small tree with a wide range in southern Arizona and northern Mexico. Different aspects of its reproductive biology have been studied by TOUMEY (1895), JOHNSON (1918), BENSON (1969a), GRANT & GRANT (1971 and unpubl.), PINKAVA & al. (1973), and others.

The flowers of *O. fulgida* are medium-sized (3–4 cm in diameter), rotate or saucer-shaped, bright magenta, and have few spreading petals. The flowers are vespertine; they open in late afternoon and last one night, withering the following morning (WHITEHEAD 1936–1937; and our observations). The plants are not floriferous; a large plant may have only 3–12 flowers blooming at any one time. However, the blooming season begins in mid June and continues through the summer (in Superior, Arizona).

The flowers are visited by pollen-collecting honeybees and unidentified medium-sized native bees in late afternoon and early morning (observations at Superior, Arizona, 1970). We suspected that the flowers might be visited and pollinated by *Xylocopa* at twilight, and *X. tabaniformis androleuca* MICHENER is a likely candidate, being principally active during these hours (HURD 1958). However, we have been unable to confirm this relationship, and more observations are needed.

The fruits are highly variable in their seed content. Some fruits contain only abortive seeds, other fruits have plump seeds. JOHNSON (1918) found that about half of the mature fruits had no sound seeds and the other half had one or more plump seeds. The number of plump seeds per fertile fruit varies from 1 to 200 (JOHNSON 1918).

The plump seeds are difficult to germinate artificially (JOHNSON 1918). Seedling plants have not been found in nature by TOUMEY (1895), JOHNSON (1918), or later investigators including ourselves. The reasons for the low variable seed fertility are unknown. *Opuntia fulgida* is diploid (PINKAVA & al. 1973) and fertile as to pollen (GRANT & GRANT 1971). In any case, seed reproduction of *O. fulgida*, in Arizona at least, is evidently very rare, and the main mode of reproduction is vegetative propagation.

Divergent modes of pollination and reproduction thus appear to have developed in some species groups of cholla cacti in the Southwest. The shifts in pollination seem to remain within the general system of bee pollination; and the changes in reproduction involve reduced reliance on bee pollination for seed set and greater emphasis on vegetative propagation. These changes affect less than half of the species of chollas in the area.

Club-Chollas

The club-chollas (*Opuntia* section *Corynopuntia*) comprise a small and subordinate group of four species in our area, as mentioned previously. Their flowers are medium-sized to moderately large, attaining flower diameters of 5 cm in *O. stanleyi* ENGELM. and *O. clavata* ENGELM., and are mostly yellow in color. They appear to be bee-pollinated flowers to judge from their general characteristics. No flower-insect records are available, however, and this is another area warranting further investigation.

Opuntia in Other Areas

The syndrome of solitary, medium to large, bowl-shaped, day-blooming flowers occurs in all southwestern species of prickly-pear Opuntias and in many or most southwestern chollas and club-chollas. It is associated with pollination by medium to large-sized bees wherever it has been studied. The same floral syndrome is widespread in *Opuntia* s. lat. in other geographical areas, where presumably it is also correlated with bee pollination, though direct observational evidence is mostly lacking.

DAUMANN's (1930) study of *O. vulgaris* (he uses the synonym *O. monacantha* HAW.) is useful in this connection. *Opuntia vulgaris* MILL. is a prickly-pear with yellow, cup-shaped, nectar-containing flowers. It is native in Brazil and Argentina, and naturalized in the Mediterranean region. DAUMANN studied it on the Mediterranean coast of France. He lists six species of bees as regular flower visitors. These are: *Apis mellifera* LINN., *Xylocopa violacea* LINN., *Ceratina cyanea* (KIRBY), *C. cucurbitina* (ROSSI), *Halictus gemmeus* DOURS., and *H. smeathmanellus* (KIRBY).

Xylocopa darwini COCKERELL has been recorded on flowers of *Opuntia echios* HOW. and *O. megasperma* HOW. in the Galapagos Islands (LINSLEY & al. 1966; HURD 1978 a).

In the American tropics, in contrast to the North American Southwest, *Opuntia* and its close relatives have produced tubular red hummingbird flowers in a few species.

A well-studied example is *Nopalea coccinellifera*, a Central American species close to *Opuntia* s. lat. and formerly included in the latter. Its flowers are red, odorless, and elongated. The petals are pressed together to form a narrow unfused tube which stands out more or less horizontally from the spiny joints. The flowers produce abundant nectar at the base. The nectar is buried 3.5–4.0 cm deep in the flowers, too deep for bees to reach, and bees are not attracted, and furthermore, there is no

landing platform for bees. The flowers are, however, well adapted for hummingbird visits (PORSCH 1938).

PORSCH (1938) observed hummingbirds (*Amazilia cinnamomea*) feeding on the flowers all day long from 6 A.M. to evening in Costa Rica. The birds carry the pollen on their foreheads. VAN DER PIJL (1937) reported that in Indonesia, where *Nopalea* is cultivated, the flowers are not visited by the indigenous flower-feeding sunbirds (*Nectariniidae*), because these birds do not hover but feed from a perch, and the spiny branches of *Nopalea* do not afford a perching place. Here the plants set few fruits, and most of the fruits contain few or no seeds (VAN DER PIJL 1937). The adaptation to American hummingbirds is thus fairly specific.

A group of species centering around *Opuntia cylindrica* DC. in the Andes have red flowers and may be hummingbird flowers. The plants are South American counterparts of the North American chollas, and are placed in the segregate genus *Austrocylindropuntia* by BACKEBERG (1970). The red-flowered species include *A. cylindrica*, *A. inarmata*, *A. exaltata*, *A. pachypus*, and others. LOEW (1904–1905) and PORSCH (1938) cite old observations of hummingbird visits to *A. cylindrica* in Ecuador; the hummingbird species are given as *Lesbia eucharis* BOURC. and *Lafresnaya flavicaudata* FRAS. The case for hummingbird flowers in this species group is suggestive and tantalizing but incomplete.

PORSCH (1938) reports hummingbirds feeding actively on the flowers of cultivated plants of *Opuntia maxima* MILL. in Costa Rica. This is a prickly-pear with large cup-shaped brownish flowers which do not appear to be specialized for hummingbirds. Among other prickly-pears for which hummingbird pollination might be predicted are the orange-flowered *O. tomentosa* S.D. of Mexico (PORSCH 1938) and red-flowered *O. quipa* WEB. of Brazil, but in general hummingbird flowers are exceptional in the prickly-pear Opuntias.

Conclusions

The available evidence indicates that the syndrome of large, solitary, diurnal, bowl-shaped flowers in *Opuntia* represents a broad adaptation to a valuable resource in the biotic environment, the bee fauna. This bee fauna is particularly rich in the Southwest (LINSLEY 1958; HURD 1978 b). The rich bee fauna here can be regarded as a broad adaptive plateau which is occupied by many species of *Opuntia*, as well as by other cacti in this region.

The result is a rather large number of species of *Opuntia* in the Southwest with the same pollination system. We are accustomed to this species pattern in some other woody genera such as *Ceanothus* (with

promiscuous insect pollination) and *Quercus* (with wind pollination). *Opuntia* provides an example of a woody genus with many bee-pollinated species. The corollary is a lack of development of floral isolation between the species. In this respect also *Opuntia* fits into the pattern known in *Ceanothus* and *Quercus*.

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